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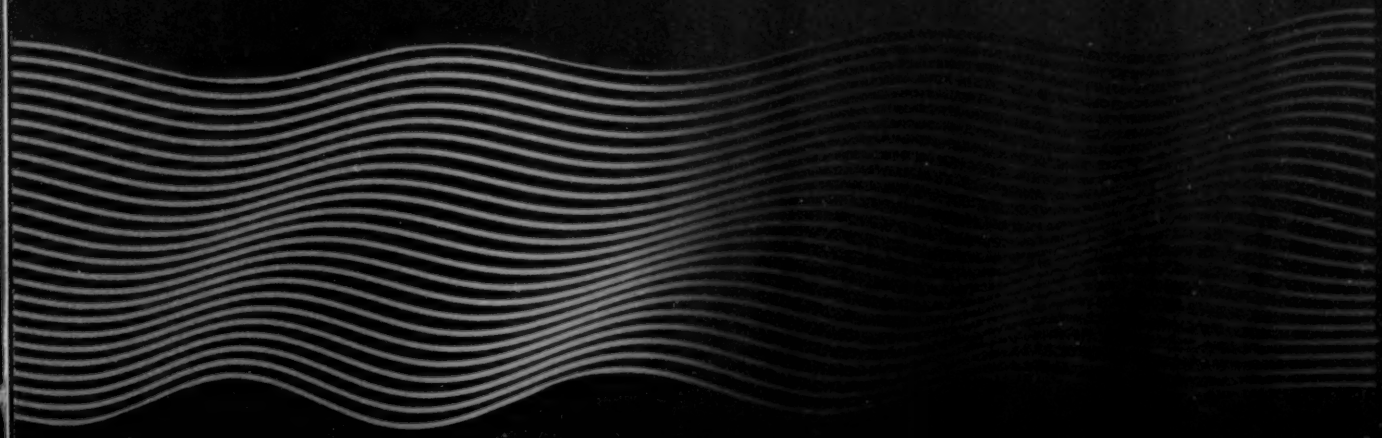

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Cyprinid fishes as samplers of benthic diatom communities in freshwater streams of varying water quality

Ted C. Rosati, Jeffrey R. Johansen, and Miles M. Coburn

Abstract: The diatom composition of natural substrates in streams of different water qualities was compared among samples collected by researchers and samples collected from the intestine contents of three species of Cyprinid fishes: *Campostoma anomalum*, *Pimephales notatus*, and *Semotilus atromaculatus*. *Campostoma* and *Pimephales* were found to be robust samplers that efficiently collected diverse, representative diatom samples. *Semotilus* were adequate diatom samplers but collected the most diverse samples. In no instance were water-quality indices calculated from *Pimephales* samples significantly different from human-collected composite samples, whereas *Campostoma* and *Semotilus* samples diverged slightly from human-collected composite samples. Internal similarities of fish-collected samples were not significantly higher than those of human-collected samples, indicating that the fish were indiscriminately foraging on diatoms. Furthermore, samples clustered primarily by stream, indicating that fish-collected samples of diatoms were as representative of the stream as those collected by human researchers. By all standards measured in this study, these three fish species sample the benthic diatom community of mid-order streams with a facility equal to that of trained ecologists.

Résumé : La composition diatomée des couches souterraines des ruisseaux, composée de différente qualité d'eau, a été compare parmi les échantillons collectionnes par les chercheurs et les échantillons collectionner dans les intestins de trois espèces de poissons: *Campostoma anomalum*, *Pimephales notatus* et *Semotilus atromaculatus*. Ca a été déduit que les *Campostoma* et les *Pimephales* sont des excellents echantillons contenant une sélection représentative des divers échantillons des diatomées. *Semotilus* par contre, était un cotillon assez adéquat, mais a collectionne une sélection diverse. Les indices de la qualité d'eau calculée des échantillons collectionner des *Pimephales* était très proche au compositions des échantillons collectionne des etres humains. Par contre, les *Campostoma* et les *Semotilus* étaient un peu diversifies des compositions des échantillons humaines. Les similarités internes des echantillons des poissons n'étaient pas différentes de manière significatives des échantillons des humains. Cela signifie que les poissons fouillaient indiscrètement sur les diatomées. D'autant plus, les échantillons étaient groupés principalement par jet d'eau dont ils proviennent, ce qui indique, que la collection des echantillons de diatomées des poissons représentent le jet d'eau comme ceux des echantillons collectionner par les rechercheures humains. De toutes les normes mesurées dans cette étude, ces les trois espèces de poissons sélectionnent une communauté de diatomées benthique des jets d'eaux moyennes, avec une facilitée égale aux écologistes professionnels.

Introduction

The use of diatoms as biomonitors is widely accepted (Barbour et al. 1999). Diatoms are known to be sensitive to organic and inorganic pollution and have documented global autoecologies with respect to pH, nutrients, organic pollution, and salinity (Round 1991; Sgro and Johansen 1995; Stevenson and Pan 1999). The first water-quality index developed for diatoms in the early 1900s, the saprobien spectrum (Kolkwitz and Marsson 1908), formed the basis of several indices currently used in Europe, Australia, and the United States (Rumeau and Coste 1988; John 1998; Barbour et al. 1999).

Using sediment cores, paleolimnologists are able to reconstruct temporal changes in water quality of lakes as a result of the excellent preservation of diatom frustules and the static nature of diatom species specific physiological tolerances and morphological characters. Numerous studies have looked at acidification and eutrophication in lakes by reconstructing diatom communities from sediment cores (Cumming et al. 1992; Hall et al. 1999; Dixit et al. 2000). This technique has also been applied to gather evidence for anthropogenic global warming (Smol and Cumming 2000).

Other methods of diatom collection are needed when conducting a paleolimnological study of a stream site where sediments are periodically washed downstream. It is accepted that diatoms are an important part of the food web, transferring light energy into toxin-free lipid-rich stores, making them a preferred source of food for herbivorous fish (Napolitano et

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al. 1996; McCollum et al. 1998). Knobloch (1991) noted that *Pimephales notatus* and *Campostoma anomalum* ingest diverse diatom floras that can be recovered from their intestines. Sray (1998) examined the diatom flora within the intestines of the Mississippi silvery minnow, *Hybognathus nuchalis*, acquired from a 30-year series of museum collections of the Pearl River, Mississippi. Sray (1998) calculated a modified Lange-Bertalot water-quality index from the diatom data to make inferences on the changes in water quality (Sray 1998). She concluded that this method of stream paleolimnology is potentially a very useful tool that requires future research. Sellman et al. (2001) expanded on Sray's methods by making comparisons between the diatoms in intestines of herbivorous minnows and human-collected benthic diatom samples within a single site. They found *C. anomalum* and *P. notatus* to be efficient collectors of diverse, representative diatom samples.

Two criteria must be fulfilled when choosing herbivorous fishes for use in paleolimnological stream studies: (*i*) herbivorous fishes should be well represented in number, distribution, and time in museum collections; and (*ii*) herbivorous fishes should be representative diatom samplers in streams of varying water quality. We chose to focus on three species of cyprinids: stoneroller minnows (*C. anomalum*), bluntnose minnows (*P. notatus*), and creek chubs (*Semotilus atromaculatus*). Trautman (1981) reported that *C. anomalum* and *S. atromaculatus* are "present in every Ohio stream capable of maintaining fish life..." and that *P. notatus* was "a most plastic species, occurring in all types of water, except deeper waters of Lake Erie and the Ohio River". These species are among the most abundant in museum collections. For example, the University of Michigan Museum of Zoology records 3215 lots of *S. atromaculatus*, 2702 lots of *C. anomalum*, and 3258 lots of *P. notatus*, with many records dating from the early 20th century.

The second criterion, determining if these herbivorous minnows are representative diatom samplers in streams of varying water quality, was the central purpose of this study. The following hypotheses were tested: (*i*) water quality of streams will not affect the representative nature of fish as samplers of diatoms, (*ii*) different species of fish do not equally collect representative samples of diatoms, based on specific feeding behavior, and (*iii*) fish samplers collect more diverse samples of diatoms than human samplers do because of a more thorough sampling of substrates throughout the site.

Materials and methods

Site descriptions

Six northeastern Ohio stream sites of different water qualities were selected for sampling. Sites were chosen based on the potential for syntopy of the three species *Campostoma anomalum*, *Pimephales notatus*, and *Semotilus atromaculatus*. Latitude and longitude were determined with a handheld global positioning system (GPS) unit (Table 1). The stream order of each site was determined using topographic map software.

All six sites contained shale rock substrate. Phelps Creek, a tributary of the Grand River, flows through undeveloped forested areas and rural residential and agricultural properties. Phelps Creek is the least developed of the six watersheds and has the greatest fish diversity. Griswold Creek and Sulfur Springs are both tributaries of the Chagrin River. The Griswold Creek and Sulfur Springs collection sites are enclosed by the thick forest of South Chagrin Reservation of the Cleveland Metroparks and semirural residential properties. Sulfur Springs is located on the western, more urbanized side of the Chagrin River.

Furnace Run and Mill Creek are dissimilar tributaries of the Cuyahoga River. The Furnace Run collection site is surrounded by rural residential properties, newer suburban developments, and parkland. Industrial parks, abandoned fields, other residential properties, and a nearby recreational park surround the Mill Creek collection site. The Northeast Ohio Regional Sewer District (1997) regarded Mill Creek as one of the most heavily enriched streams in the greater Cleveland area, often subject to sanitary sewer overflows and discharges. Euclid Creek, a tributary of Lake Erie, is also a heavily enriched stream. Forest, field, and cliffs of the Euclid Creek Reservation of the Cleveland Metroparks surround the Euclid Creek collection site. The surrounding area can be classified as parkland and urban residential and commercial properties.

Water chemistry and physical parameters

Water chemistry samples and physical water parameters were collected approximately 3 weeks before and including the date of the diatom and fish sampling for all sites (except Euclid Creek) on 27 July and 4, 11, and 15 August 2000. Water chemistry samples and physical water parameters were only collected on the date of diatom and fish sampling for Euclid Creek (21 August 2000).

Before the actual diatom and fish sampling at each site, water chemistry samples were collected in one acid-washed 500-mL and one acid-washed 1000-mL polyethylene water bottle at each site. Water samples were then frozen for later testing of total suspended solids, nitrate, nitrite, ammonia, total nitrogen, reactive phosphate, total phosphorus, silica, sulfate, alkalinity, and water hardness using methods described for the Texas Instruments calculator-based lab (CBL) system (Johnson et al. 1999).

Readings of physical water parameters were metered at the sites. Temperature (°C), salinity (‰), and conductivity (μS) readings were taken with a YSI 30 probe; pH was taken with a Barnant probe, and dissolved oxygen ($mg \cdot L^{-1}$) readings were taken with a YSI 90 probe. Additional water samples were collected using specialized glass bottles for biological oxygen demand (BOD). The bottles were stored in a dark chamber at 20–22°C, and a dissolved oxygen reading ($mg \cdot L^{-1}$) was taken 5 days after collection with the YSI 90 probe. BOD was then recorded as the difference between the dissolved oxygen reading taken on the collection date and the reading taken 5 days later (Johnson et al. 1999). Nephelometric turbidity units (NTU) were determined only for the date of diatom sample collection.

Diatom and fish acquisition

The benthic diatom sampling was conducted by standard methods (Sgro and Johansen 1995). Five benthic samples were collected at each site. Each individual sample consisted of a proportional collection of 10 total rock or wood sub-

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Table 1. Physical characteristics of the streams and mean values of selected water column chemical and biological characteristics.

Characteristic	Furnace Run	Mill Creek	Griswold Creek	Sulfur Springs	Phelps Creek	Euclid Creek
Latitude (41°N)	25′31″	25′4″	27′23″	25′31″	31′59″	33′51″
Longitude (81°W)	38′19″	38′18″	24′11″	25′3″	57′49″	31′58″
Elevation (m)	305	183	244	249	299	209
Stream order	3	3	2	2	4	3
TSS ($mg \cdot L^{-1}$)	37.8bc	40.5c	35.8bc	17.0abc	11.5ab	1.4a
Conductivity (μS)	990c	1178d	694b	679b	394a	815bc
Turbidity (NTU)*	7.5	50.0	3.5	4.5	7.0	4.4
pH	7.66a	7.45a	8.26b	8.23b	8.21b	8.36b
BOD ($mg \cdot L^{-1}$)	0.17	1.20	0.26	–0.13	1.11	1.38
DO ($mg \cdot L^{-1}$)	7.54a	7.42a	8.72ab	8.65ab	8.83ab	10.08b
Total P ($\mu g \cdot L^{-1}$)	43.3	67.7	33.3	60.0	113.3	200.0
PO_4 ($\mu g \cdot L^{-1}$)	112.5a	42.5a	50.0a	85.0a	55.0a	266.7b
Total N ($\mu g \cdot L^{-1}$)	625	1950	1300	275	375	540
NO_3 ($\mu g \cdot L^{-1}$)	275a	1550b	225a	600a	350a	1267b
NO_2 ($\mu g \cdot L^{-1}$)	1.25a	166.75b	0.75a	1.25a	1.25a	7.00a
NH_4 ($\mu g \cdot L^{-1}$)	17.5a	425.0b	22.5a	20.0a	22.5a	3.3a
SiO_2 ($mg \cdot L^{-1}$)	6.59cd	6.19cd	5.24bc	6.96d	3.51a	3.81abc
SO_4 ($mg \cdot L^{-1}$)	70.0cd	78.0d	60.0bc	55.8b	29.3a	67.5bcd
Alkalinity ($mg \cdot L^{-1}$)	193b	214b	203b	135a	123a	112a
Hardness ($mg \cdot L^{-1}$)	259bc	324c	248b	157a	142a	212ab

Note: Values in rows differ significantly if they share no common letters. Significant differences not detected in parameters without letters. Codes for parameters: BOD, biochemical oxygen demand; DO, dissolved oxygen; NTU, nephelometric turbidity units; TSS, total suspended solids.

*Single replicate taken, analysis of variance and least significant difference tests not run.

strates to give an accurate representation of the site (Sgro and Johansen 1995). The collection was conducted within a transect perpendicular to the course of the stream, and samples were later frozen in sequence to preserve the collected diatoms for later identification.

Fishes were collected with seines and by electroshocking. The collection consisted of only *C. anomalum*, *P. notatus*, and *S. atromaculatus*. Approximately 10 specimens of each species when present were collected at each of the six sites. The fishes were then labeled, measured for standard length, and preserved in 50% ethyl alcohol. Although Furnace Run, Mill Creek, and Sulfur Springs were all suitable habitat for *P. notatus* and *S. atromaculatus*, we did not find both species in those streams. Euclid Creek was added late in the study to provide an additional polluted site for water-quality comparisons.

Preparation of permanent diatom slides

Preparation of the benthic diatoms was conducted using standard methods (Sgro and Johansen 1995). Preparation of fish samples was slightly different. Incisions were made from the anus on either side to the pectoral fins. The entire intestine and stomach from the esophagus to the anus was removed and then rinsed with deionized water on the outside. The intestines were placed into a beaker with 20 mL deionized water and 10 mL of nitric acid were added. The samples were then prepared using standard techniques for benthic diatoms (Sgro and Johansen 1995). Several of the *S. atromaculatus* pellets required an extraction using ethyl acetate to isolate the diatom pellet from unwanted fats. One permanent slide from each sample was selected and counted under an oil-immersion lens at 1000× on a Zeiss Axioskop photomicroscope with Nomarski DIC optics. More than 400 valves were counted and identified to species from each slide following the taxonomic treatments of Patrick and Reimer (1966, 1975) and Krammer and Lange-Bertalot (1986, 1988, 1991*a*, 1991*b*).

Data analysis

A cluster dendrogram based on Ružička's similarity index (Ružička 1958; Pielou 1984) including all species was used to determine similarity of the diatom community among sites and samplers. This method has been used extensively in ecological studies because it introduces less distortion than other methods (Kaesler and Cairns 1972). The UPGMA (unweighted pair-group method with arithmetic means) cluster analysis (Pielou 1984) was conducted using a noncommercial, unpublished software program. Centered principal components analysis (PCA) was conducted for both water chemistry and dominant species based on correlation matrices (Pielou 1984). Water chemistry data were standardized. The PCA based on 18 important species (as defined by Douglas and Smol 1995) was not standardized. Shannon diversity and species richness were also compared among samplers within stream sites using analysis of variance (ANOVA). These analyses determined if fishes were representative collectors of the diatoms in the stream. Six water-quality indices were calculated for each sample to enable comparison of the accuracy and precision of fish samplers to human samplers: the Lange-Bertalot index (LBI; Lange-Bertalot 1979); the generic diatom index (GDI; Rumeau and Coste 1988); the trophic diatom index (TDI; Kelly and Whitton 1995); the tolerant species index (TSI; Kelly and Whitton 1995); the sensitive species index (SSI; Kentucky Department of Environmental Protection 1993); and the Erie diatom index (EDI; Sgro and Johansen 1998). Each index was then compared among sample types

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using ANOVA combined with a least significant difference (LSD) multiple comparisons test.

Results

Stream water chemistry

This study was designed to measure the representative nature of fishes as samplers of diatoms in streams of varying water quality. The six streams studied did vary in their water chemistry and physical parameters. There were significant differences in the levels of a number of chemical characteristics (Table 1). Dissolved oxygen ($p = 0.042$), conductivity ($p < 0.001$), silica ($p = 0.002$), alkalinity ($p < 0.001$), and hardness ($p = 0.002$) were significantly different among streams (Table 1). Differences in nitrate levels were significant ($p = 0.001$), with the LSD test indicating significantly higher levels in Mill Creek and Euclid Creek. The differences among ammonium and nitrite levels were significant ($p < 0.001$), with Mill Creek samples at least 20 times higher than the other streams (Table 1). Differences in reactive phosphate levels were significant ($p = 0.048$), with Euclid Creek having significantly higher levels than the other streams (Table 1). Turbidity levels were considerably higher in Mill Creek. Total suspended solids, total nitrogen, and total phosphorus levels were not significantly different among streams (Table 1). Total N and P were unexplainably lower than dissolved N and P in some streams.

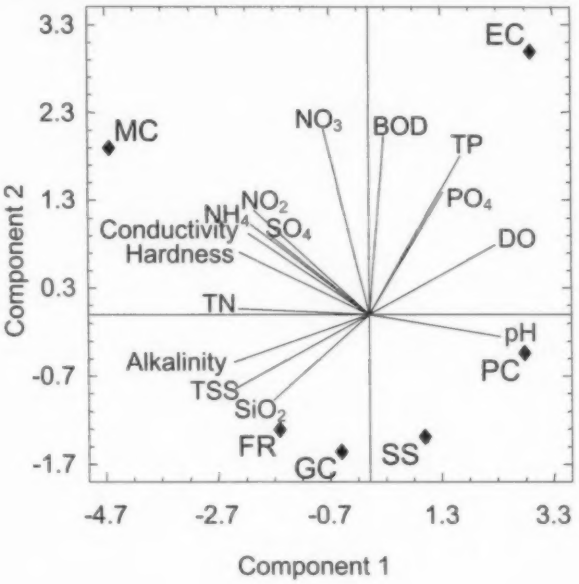
PCA was run on the water chemistry and physical parameters (Fig. 1). The first axis, which explains 55.5% of the variation, appears to be weighted by basin-specific differences in geology and hydrology, whereas the second axis, which explains 25.5% of the variation, seems to be correlated with nutrient enrichment. The results showed that Euclid Creek and Mill Creek had higher levels of phosphorus, nitrogen, and BOD, possibly indicating eutrophication. Euclid Creek and Mill Creek varied in alkalinity and conductivity. The PCA indicated that the other four streams (Furnace Run, Phelps Creek, Griswold Creek, and Sulfur Springs) had intermediate levels of various water-quality parameters.

All water-quality indices showed significant differences among streams when all samples were analyzed (Table 2). The LSD multiple comparisons test indicated that Mill Creek was the most polluted stream, with elevated pollution in Euclid Creek (Table 2). These results coincide with the results of the water chemistry analysis (Table 1; Fig. 1). The SSI unexpectedly indicated Sulfur Springs to be the most polluted site, which contradicts the other five indices (Table 2). Before sampling, we observed flooding of the pool that significantly altered the Sulfur Springs site, possibly reducing the number of sensitive species present.

Diatom community composition in streams

A total of 207 diatom taxa were recorded from the 90 samples from the six streams (Rosati 2001). However, the number of taxa recorded in a count of only 400 valves averaged 32 per count and ranged from a low of 12 species in Euclid Creek to a high of 50 species in Phelps Creek. To answer the question of the representative nature of fish as samplers of diatoms in different streams, differences in diatom communities were analyzed. The cluster dendrogram revealed that stream site was more important than the sampler type in determining species composition observed in the sample (Fig. 2). PCA run on these important species also showed that samples primarily clustered by stream (not shown, see Rosati 2001).

Fig. 1. Principal components analysis biplot of water chemistry parameters and the six streams. The first axis explains 55.5% of the variation and the second axis explains 25.5% of the variation. Codes for streams: FR, Furnace Run; MC, Mill Creek; GC, Griswold Creek; SS, Sulfur Springs; PC, Phelps Creek; EC, Euclid Creek. Codes for parameters: BOD, biological oxygen demand; DO, dissolved oxygen.



Fish as samplers of diatom communities

The arrangement of sampler type within each stream of the cluster dendrogram indicated that *P. notatus* samples were the most similar to human-collected samples in two of the three sites with all sampler types (Fig. 2; Euclid Creek, Griswold Creek). The third site, Phelps Creek, showed both *P. notatus* and *C. anomalum* samples as being similar to human-collected samples (Fig. 2). The cluster was also run two more times with four replicates randomly selected from each sample type and then three replicates randomly selected from each sample type. Stream continued to be the most important factor determining the clusters, indicating that three or four replicates might be an adequate sample. Ružička's similarity gives generally low values, as evidenced by the fact that the maximum similarity among the 180 comparisons made from all streams was only 69% (Fig. 2).

Comparisons of mean internal similarity were made among the four sampler types in Euclid Creek, Phelps Creek, and Griswold Creek, the streams containing all three species. Internal similarity is the similarity among diatom communities collected by one sampler type within each stream. Differences in overall internal similarity among samplers in these three streams were significant ($p < 0.001$). Mean internal similarity of human-collected samples (49.9%) was not sig-

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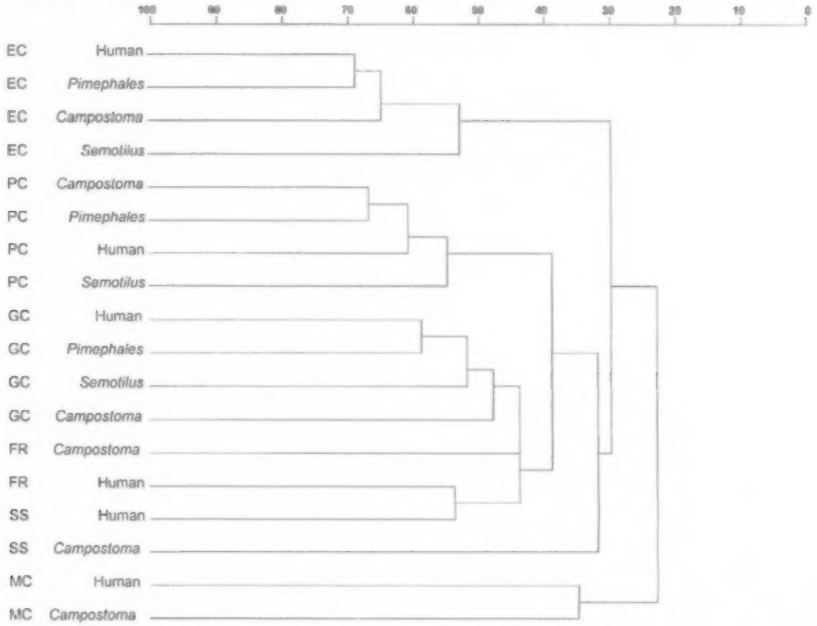
Table 2. Means for sample characteristics among four sample types.

	RICH	SHAN	LBI	GDI	TDI	TSI	SSI	EDI
Site								
Furnace Run	33.2b	3.75b	2.44c	2.52bc	4.26abc	0.55abc	0.17c	9.20c
Mill Creek	32.1ab	3.74b	1.81a	2.22b	3.81a	0.68c	0.14bc	6.40a
Griswold Creek	30.8ab	3.38b	2.67c	2.53c	4.24c	0.50ab	0.13ab	8.00b
Sulfur Springs	30.1ab	3.38b	2.49bc	2.78c	4.46d	0.53bc	0.07a	6.80a
Phelps Creek	42.1c	4.31c	2.43b	2.83c	4.02bc	0.46ab	0.18b	9.60b
Euclid Creek	27.3a	2.80a	2.29b	1.52a	3.99abc	0.86d	0.12ab	8.00b
Sampler								
Human	33.3a	3.57a	2.35	2.40a	4.13ab	0.60b	0.14	8.00
Campostoma	29.8a	3.34a	2.46	2.74bc	4.07ab	0.49a	0.16	8.73
Pimephales	32.6a	3.51a	2.41	2.44ab	4.19b	0.51a	0.13	8.40
Semotilus	38.5b	3.92b	2.47	2.63bc	3.98a	0.48a	0.15	9.20

Note: Codes for indices: RICH, species richness; SHAN, Shannon diversity; LBI, Lange-Bertalot index; GDI, generic diatom index; TDI, trophic diatom index; TSI, tolerant species index; SSI, sensitive species index; EDI, Erie diatom index. Values in columns of site or sampler differ significantly if they share no common letters. Letters are not reported if not significantly different.

Fig. 2. Cluster dendrogram of all samples based on Ružička's similarity index. Codes for streams: FR, Furnace Run; MC, Mill Creek; GC, Griswold Creek; SS, Sulfur Springs; PC, Phelps Creek; EC, Euclid Creek.



nificantly different from that of *P. notatus* samples (49.7%) but was significantly higher than mean internal similarity in *C. anomalum* (36.3%) and *S. atromaculatus* (33.8%) samples. Within each stream, mean internal similarity of human-collected samples was not significantly different from either *Campostoma* or *Pimephales* samples (Fig. 3).

Between-sampler similarity is the comparison of similarity values between sampler types within a single site, indicating possible differences in fish species as samplers of diatoms. In the three streams containing all samplers, *P. notatus* samples always had the highest between-sampler similarity to human-collected samples, followed by *C. anomalum* and *S. atromaculatus* samples (Fig. 4). The between-sampler similarity of human-collected samples to *P. notatus* samples averaged 42.3%. In Phelps Creek, *Pimephales* samples had a higher between-sampler similarity to human-collected samples (41.2%) than the internal similarity of the human-collected samples (40.3%). Surprisingly, this shows that human-collected samples in Phelps Creek were more similar to *P. notatus* samples than they were to themselves. *Campostoma* between-sampler similarity to human-collected samples averaged 40.7% in the three streams where all fish were present and an overall between-sampler similarity of 36.3% in all six streams. *Semotilus* between-sampler similarity to human-collected samples averaged 38.2% (Fig. 4).

The differences among species richness and Shannon diversity by sampler were significant ($p = 0.002$). *Semotilus atromaculatus* samples had significantly higher richness and

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Fig. 3. Mean (± standard error) internal similarity (based on Ružička's similarity index) for all streams. Samplers within each stream differ significantly if they share no common letters. Designation of sampler types: human, solid bars; *C. anomalum*, open bars; *P. notatus*, shaded bars; *S. atromaculatus*, open bars with diagonal stripes.

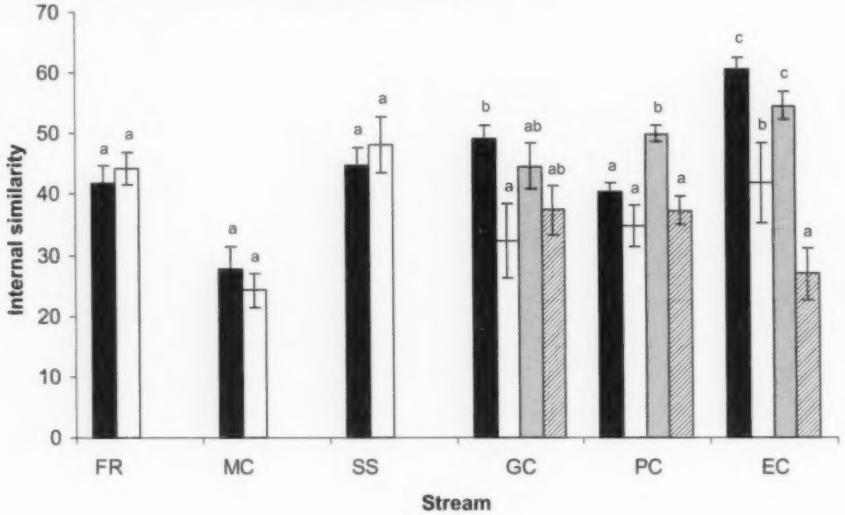
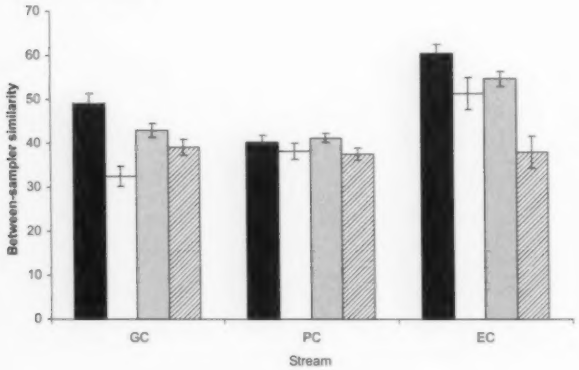


Fig. 4. Mean (± standard error (SE)) between-sampler similarity (based on Ružička's similarity index) for Griswold Creek, Phelps Creek, and Euclid Creek. Mean (±SE) internal similarity of the human sampler is reported for comparison purposes. Designation of sampler type: human, solid bars; *C. anomalum*, open bars; *P. notatus*, shaded bars; *S. atromaculatus*, open bars with diagonal stripes.



diversity than the *C. anomalum*, *P. notatus*, and human-collected samples (Table 2). *Semotilus* also had the lowest mean internal similarity (Fig. 3) of all samplers (33.8%), possibly in part because of the high diversity in the samples.

Fish-sampled diatom flora as a water-quality indicator

Within each stream, no water-quality indices showed significant differences between *P. notatus* samples and human-collected samples (Table 3). Means of water-quality indices were analyzed within each stream among sampler types to further specify which sampler collected the most representative sample of diatoms. Sulfur Springs water-quality indices means showed significant differences between *C. anomalum* samples and human-collected samples only in the GDI. In Furnace Run, significant differences were found between *C. anomalum* samples and human-collected samples in all but one water-quality index, LBI (Table 3). In Griswold Creek, significant differences were found between *S. atromaculatus* and human-collected samples in only the LBI and between *C. anomalum* and human-collected samples in the LBI, GDI, and TSI (Table 3). In Euclid Creek, significant differences were also detected between *Semotilus* and human-collected samples for the GDI and TSI (Table 3).

There were no significant differences among any samplers in the means of the water-quality indices in the most polluted stream studied, Mill Creek, and one of the cleanest streams studied, Phelps Creek (Table 3). The other heavily polluted stream, Euclid Creek, showed no significant differences among samplers except *S. atromaculatus* samples, which indicated cleaner conditions (Table 3). Griswold Creek, one of the cleanest streams studied, showed no significant differences between human-collected samples and *P. notatus* samples, but significant differences were found between human-collected samples and the other two fish samplers (Table 3).

Discussion

The objective of this study was to measure the representative nature of fish as samplers of diatoms in streams of varying water quality with the intent of using the diatom samples as a means of conducting current and paleolimnological water-quality assessments. We conclude that all three species of fish (*Campostoma anomalum*, *Pimephales notatus*, and *Semotilus atromaculatus*) are representative samplers of diatoms in mid-order streams. As predicted, water quality of streams did not seem to affect the ability of fish to collect a representative sample of diatoms. Fishes collected diverse samples of diatoms, as evidenced by the mean richness and

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Table 3. Means for sample characteristics among four sample types and six streams.

Stream	Sampler	RICH	SHAN	LBI	GDI	TDI	TSI	SSI	EDI
FR	Human	35.4b	3.85	2.44	2.52a	4.23b	0.553b	0.166a	9.2a
	Campostoma	31.0a	3.65	2.68	3.00b	3.77a	0.389a	0.296b	12.0b
MC	Human	32.6	3.82	1.81	2.22	3.81	0.684	0.140	6.4
	Campostoma	31.6	3.66	2.20	2.75	3.80	0.545	0.186	7.6
SS	Human	32.4	3.53	2.49	2.77a	4.47	0.525	0.074	6.8
	Campostoma	27.8	3.24	2.33	2.98b	4.54	0.620	0.094	7.2
GC	Human	29.0a	3.30b	2.67b	2.53a	4.24ab	0.503b	0.132	8.0
	Campostoma	22.6a	2.73a	2.89c	3.03b	4.34b	0.232a	0.092	8.8
	Pimephales	28.2a	3.22b	2.69b	2.74ab	4.39b	0.363ab	0.118	8.0
	Semotilus	43.4b	4.27c	2.51a	2.91ab	3.89a	0.415b	0.156	9.6
PC	Human	44.6b	4.42ab	2.43	2.82	4.02	0.464	0.176	9.6
	Campostoma	36.8a	3.93a	2.38	2.80	4.00	0.427	0.164	9.2
	Pimephales	40.8ab	4.24ab	2.31	2.80	4.17	0.408	0.130	8.4
	Semotilus	46.2b	4.67b	2.35	2.83	4.10	0.433	0.128	8.4
EC	Human	25.6	2.50	2.29ab	1.52a	3.99	0.862b	0.124	8.0ab
	Campostoma	28.8	2.86	2.29ab	1.87ab	3.99	0.728ab	0.118	7.6a
	Pimephales	28.8	3.06	2.24a	1.77ab	4.00	0.768ab	0.154	8.8ab
	Semotilus	25.8	2.81	2.56b	2.16b	3.97	0.589a	0.174	9.6b

Note: Codes for streams: FR, Furnace Run; MC, Mill Creek; GC, Griswold Creek; SS, Sulfur Springs; PC, Phelps Creek; EC, Euclid Creek. Codes for indices: RICH, species richness; SHAN, Shannon diversity; LBI, Lange-Bertalot index; GDI, generic diatom index; TDI, trophic diatom index; TSI, tolerant species index; SSI, sensitive species index; EDI, Erie diatom index. Values in columns of each stream differ significantly if they share no common letters.

Shannon diversity, which were comparable to human-collected samples but significantly higher in *Semotilus* samples. The samples clustered by stream primarily, indicating that fish-collected samples of diatoms are as representative as those collected by researchers. Therefore, it seems likely that the use of fish as samplers of diatoms may well be a superior sampling methodology.

The different species were all adequate representative samplers but did not collect equally representative samples of diatoms. Contrary to Sellman et al. (2001), *Pimephales* and human-collected composite samples were the most representative samples, followed by *Campostoma* and *Semotilus* samplers. The precision of the sampler replicates in each stream, measured as internal similarity, was not significantly different between *P. notatus* and human-collected composite samples but was significantly greater than *C. anomalum* and *S. atromaculatus* samples. This indicates that the fish samplers were not foraging on selected diatoms but were collecting diverse, random samples. Overall, fish samplers had higher mean internal similarity than human-collected samples in three of the six streams. Sellman et al. (2001) concluded that *C. anomalum* were excellent samplers of diatoms in Sulfur Springs, which did correspond to the findings of this study where the mean internal similarity of their samples was greater in Sulfur Springs than the human-collected composite samples. However, Sulfur Springs is a relatively unusual site, cut off upstream by a 2-m waterfall and downstream by a relatively shallow output into the higher-order Chagrin River. Adequate diatom pellets were also difficult to extract from the omnivorous *S. atromaculatus*. Its samples indicated that they were not actively feeding on diatoms. Additional *Semotilus* samples had to be prepared to ensure that we had five slides with an adequate density of diatoms. This made *S. atromaculatus* less desirable as diatom samplers.

The diatom flora sampled from the intestines of fish can be applied to stream water-quality monitoring. The water-quality indices calculated from the intestinal contents of all fish samplers indicated cleaner conditions than human-collected samples. It seems that the differing water quality of streams did not affect the ability of *P. notatus* to act as effective samplers of diatoms. None of the water-quality indices was significantly different between *P. notatus* and human-collected samples. The other two species were adequate in terms of water-quality assessment, rarely showing significant differences from human-collected samples in most of the streams.

Using fish as samplers of diatoms might potentially replace current methods that phycologists use to determine diatom assemblages and water quality in streams. This study indicated that fishes are as good as human researchers at collecting composite diatom samples. Disadvantages in composite samples of natural substrates are the subjective nature of collection, the difficulty in effectively sampling certain locations (i.e., bedrock, shifting substrates, or high velocity streams), and the requirement of experienced specialists for sampling (Barbour et al. 1999). Using herbivorous fishes as diatom samplers also has advantages over use of artificial substrates as samplers by eliminating subjectivity in selection of habitat and sample sites within the stream (Barbour et al. 1999). Disadvantages in sampling using artificial substrates are as follows: (*i*) they require two trips to each site (one to set and one to retrieve); (*ii*) artificial substrates may not be representative as a result of different microhabitats offered on the substrate; and (*iii*) sampler loss or vandalism commonly occurs and samplers may be awkward to transport and store (Barbour et al. 1999).

Although fishes are excellent samplers for diatoms to be used in determining diatom assemblages and in water-quality monitoring, there are some applications in which human re-

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searchers are clearly superior. If it is important to sample and characterize the diatoms from diverse substrates (macrophytic algae, rocks, wood, sediment), then researchers must be used as fishes collect only a composite sample. If diatom composition is to be combined with quantitation (chlorophyll *a* or biovolume per unit area of substrate), then fish samplers are again inadequate. Thus, for ecological studies in general, fish are likely not the best choice as a sampler. If a stream has very diverse substrates, it is possible that researchers could obtain greater species richness than herbivorous minnows (although this is contrary to our experience so far).

Fishes are only clearly advantageous (and possibly superior) when the intent is to sample stream diatoms for water-quality monitoring. Thus, they may have great utility in illuminating recent paleolimnology of streams and are the only means of recovering this information from streams or stream sections lacking historical data on water quality. For example, Sray (1998) used museum specimens of *Hybognathus nuchalis* to reconstruct the changes in diatom composition at a stream site over a 30-year period. This demonstration project showed a sharp decrease in water quality over time at a single site in the Pearl River, Mississippi.

The distributions of the three species in this study are widespread east of the Mississippi River (Cooper 1983) and are ubiquitous and abundant in museum collections. Their use as water-quality indicators could potentially be applied over a broad area in North America. Apparently *P. notatus*, *C. anomalum*, and *S. atromaculatus* are virtually interchangeable as samplers of diatoms, suggesting that any species with similar life history traits would also be a representative sampler of diatoms. The only apparent disadvantage of using fish as samplers of benthic diatoms is the requirement of fish collection and identification. However, because herbivorous fish samplers seem to be interchangeable, fish identification may only require collecting fish that display cyprinid herbivorous fish characters such as minnow-like bodies and subterminal mouths. Therefore, the use of herbivorous fishes as representative samplers of diatoms could potentially be used to uncover a plethora of stream paleolimnological water-quality data that was previously unavailable.

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Physiological energetics of Lake Erie dreissenid mussels: a basis for the displacement of *Dreissena polymorpha* by *Dreissena bugensis*

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Abstract: I measured respiration, shell growth, body mass, and reproduction in sympatric populations of zebra (*Dreissena polymorpha*) and quagga (*Dreissena bugensis*) mussels in western Lake Erie to determine if the species differ in physiological parameters and if any differences provide an explanation for the recent displacement of zebra mussels by quagga mussels. Between May and August, I measured respiration (1998), shell growth of marked mussels suspended in cages in the lake (1999–2000), soft body mass and mass of gametes released (1998–2001), and the number of gametes released by individual mussels (1999). Quagga mussels had lower respiration rates and greater shell growth and body mass. There was no difference in the percentage of spawning mussels or the number of sperm released by individuals, but zebra mussels generally released more eggs and a greater mass of gametes than did quagga mussels. Similar reproduction at a lower body mass indicates that zebra mussels devote a greater proportion of body tissue to reproduction. Lower respiration rates and larger size give quagga mussels a competitive advantage and may explain their displacement of zebra mussels.

Résumé : Des mesures de la respiration, de la croissance de la coquille, de la masse corporelle et de la reproduction chez des populations sympatriques de moules zébrées (*Dreissena polymorpha*) et de moules quagga (*Dreissena bugensis*) dans l'ouest du lac Érié m'ont servi à déterminer si ces espèces diffèrent par leurs paramètres physiologiques et si certaines de ces différences peuvent expliquer le remplacement récent des moules zébrées par les moules quagga. Les mesures prises entre mai et août incluent la respiration (1998), la croissance de la coquille de moules marquées et suspendues dans des cages dans le lac (1999–2000), la masse des parties molles du corps et celle des gamètes libérées (1998–2001), ainsi que le nombre de gamètes libérées par individu (1999). Chez les moules quagga, le taux respiratoire, la croissance de la coquille et la masse corporelle sont plus faibles. Il n'y a pas de différence dans le pourcentage de moules qui frayent ou le nombre de spermatozoïdes libérés par individu, mais les moules zébrées libèrent en général plus d'oeufs et une masse plus importante de gamètes que les moules quagga. La reproduction semblable malgré une masse corporelle plus petite indique que les moules zébrées consacrent une proportion plus élevée de leurs tissus à la reproduction. Les taux respiratoires plus bas et la taille plus élevée donnent un avantage compétitif aux moules quagga et expliquent peut-être pourquoi elles remplacent les moules zébrées.

[Traduit par la Rédaction]

Introduction

Establishment of dreissenid mussel populations have caused many recent changes in the Great Lakes and have had significant impacts on food webs of numerous invaded lakes, reservoirs, and rivers (Schloesser and Masteller 1999; Stewart et al. 1999; Bially and MacIsaac 2000). As a new primary consumer in an invaded system, zebra mussel (*Dreissena polymorpha*) consumption of phytoplankton depends on population density and, when estimated by seasonal energetics measurements (Stoeckmann and Garton 1997) or by bioenergetics models (Madenjian 1995), may be as high as 50% of seasonal primary production. In addition, the impact of zebra mussels extends to alteration of benthic communities (Gonzalez and Downing 1999; Stewart et al. 1999) and includes competing with, and in some areas eliminating, native unionid populations (Mackie 1991; Schloesser and Masteller 1999).

In addition to zebra mussels, a second dreissenid, the quagga mussel (*Dreissena bugensis*), is expanding its range in Lake Erie from east to west (Mills et al. 1999; Jarvis et al. 2000). Initially found primarily in deeper, cooler waters, quagga mussels can survive (MacIsaac 1994) and are present in shallow, warmer waters (Mitchell et al. 1996). In addition to their range expansion, quagga mussels are slowly displacing zebra mussels and are becoming the dominant dreissenid (Mills et al. 1999). For example, densities of quagga mussels in the shallow, warmer western basin of Lake Erie have increased from 20% of the dreissenid population in 1998 to 80% in 2001 (A. Stoeckmann, unpublished data).

Zebra and quagga mussels are benthic suspension feeders with very similar life style and habitat and food require-

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ments. Competitive exclusion predicts that species with the same resource requirements cannot occupy the same niche and species with a high degree of niche overlap must be competitors (Hutchinson 1957). Thus, species competing for resources cannot coexist (Hutchinson 1957). Therefore, sympatric populations of zebra and quagga mussels must experience a high degree of niche overlap. The displacement of zebra mussels by quagga mussels implies that quagga mussels must possess some characteristic that gives them an advantage in their competition with zebra mussels. Because they are so similar in lifestyle, the displacement of zebra mussels by quagga mussels may be due to differences in their physiology. Previous studies have shown some differences in the biology of zebra and quagga mussels. Growth differs with quagga mussels becoming larger than zebra mussels (Mills et al. 1999; Jarvis et al. 2000). Reproductive timing may differ; quagga mussels mature eggs at lower temperatures than do zebra mussels (4.8°C for quagga mussels vs. 12°C for zebra mussels; Roe and MacIsaac 1997). Metabolic functioning of the mussels may also differ, as suggested by lower tolerance of high temperatures in quagga mussels (Domm et al. 1993; Spidle et al. 1995). Any difference between the mussels must be important because the displacement of zebra mussels by quagga mussels implies that quagga mussels have physiological or behavioral characteristics that give them a competitive advantage over zebra mussels.

The primary objectives of this study were (*i*) to compare respiration, growth, and reproduction in sympatric populations of zebra and quagga mussels in western Lake Erie to determine if the species differ in specific physiological parameters and (*ii*) to provide an explanation for the recent displacement of zebra mussels by quagga mussels in western Lake Erie if any differences were found.

Material and methods

Zebra and quagga mussels were collected and measured at F.T. Stone Laboratory, Ohio State University, South Bass Island, western Lake Erie. Throughout the study period, mussels were collected by scuba from a depth of 4–5 m near the field station, removed from the rocks, and held in running lake water aquaria at ambient temperatures until used (<24 h). To determine differences between species in their basic physiology, I measured energy budget components, including respiration, body mass, shell growth, and reproductive output.

To estimate respiration I measured oxygen consumption ($\mu L\ O_2 \cdot h^{-1}$) using a Gilson differential respirometer and standard manometric techniques. Oxygen consumption was measured five times at about 3-week intervals during May–August 1998 for individual mussels (n = 17–19 of each species) over a size range (shell length 10–26 µm). During the measurements, mussels were held in filtered lake water (glass-fiber filters, type AE, 1.0 µm) at ambient lake water temperature and oxygen consumption was measured for 4 h.

To track changes in body mass over the season and between years, I measured shell length and soft tissue mass of mussels five times during May–August 1998, mid-summer (June) in 1999, five times during May–August 2000, and three times during April–August 2001. Mussels were newly collected each time and in 1998 were the same mussels used in respiration measurements. Shell lengths of mussels 5–32 mm were measured with Vernier calipers (nearest 0.1 mm, n = 19–44 of each species). Soft tissue was separated from the shell, dried in preweighed foil pans at 65°C for 24 h, and reweighed (nearest 0.1 mg).

I measured individual shell growth of mussels by holding them in cages suspended in the lake for 386 days during July 1999 – August 2000. I uniquely labeled mussels over a size range (7–28 mm, n = 165 of each species) with colored, numbered tags and measured initial shell lengths. After marking and measuring, equal numbers and size ranges of each species were put into three plastic mesh cages (13 cm long × 10 cm diameter, 2 mm pore size, n = 110 per cage). The cages were individually suspended 1 m above the lake bottom in water 3.5 m deep. Cages were inspected and cleaned about biweekly with scuba (July–October 1999 and May–August 2000). I retrieved the cages at the end of July 2000 and measured surviving mussels' final lengths and dry body mass as described above.

Reproduction was measured in two ways: (*i*) the mass of gametes released by freshly collected mussels and (*ii*) the number of gametes released by individual mussels induced several times over a season. I induced spawning for all reproduction measurements with 1 mM serotonin (5-hydroxytryptophan) in 20 mL of filtered lake water (glass-fiber filters, type AE, 1.0 µm pore size).

To monitor reproduction in the general population, I induced spawning and weighed the mass of gametes released. I induced mussels in a size range (10–32 mm) at various times during the season between 1998 and 2001: four times during May–July 1998, once in June 1999 in addition to following individual spawning (see description below), three times during June–July 2000, and three times during April–July 2001. After 3 h of induction, sex was determined and gametes were collected on preweighed membrane filters (0.45 µm pore size). Filters were dried at 65°C for 24 h, cooled in a desiccator, and reweighed. I measured the shell lengths of all induced mussels. Body mass of induced mussels was estimated using length – body mass regressions measured on separate sets of mussels collected on each induction date.

Spawning was induced four times during June–July 1999 and the gametes released were counted to determine the number of gametes produced by individual mussels over a season (Table 1). Mussels over a size range (10–28 mm) were induced to spawn for 2 h (n = 33 zebra mussels and 34 quagga mussels) and then transferred into 50 mL of filtered lake water for one to three postinduction intervals. At the completion of the first set of postinduction intervals, I determined sex, individually marked all of the mussels with coloured, numbered tags, and measured shell lengths. Between inductions, the marked mussels were held in running lake water aquaria at ambient lake temperatures. Mortality during the 2 months was low (1.5%).

I counted gametes released during inductions and postinduction periods. I counted eggs with a counting chamber (two 1-mL samples) and sperm with a hemocytometer. I estimated beginning body masses using length – body mass regressions for a separate set of mussels collected at the beginning of the experiment.

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Table 1. Schedule of spawning inductions, postinduction collection periods, and percentage of mussels that spawned when individual Lake Erie zebra and quagga mussels were induced several times during the season (June–July 1999).

					Spawners (%)			
					Females		Males	
I	Days between inductions	No. of PI transfers	Total PI time (h)	Number of mussels (zebra, quagga)	Z	Q	Z	Q
1		3	22	67 (33, 34)	100	100	100	100
2	1	2	14	67 (33, 34)	100	95	100	92
3	3	1	5	67 (33, 34)	80	67	67	62
4	20	1	5	64 (33, 31)[a]	67	67	83	46

Note: I, induction; PI, postinduction; Z, zebra mussel; Q, quagga mussel.
[a]Number of mussels decreased by death.

Statistical analyses

I used ANCOVA (analysis of covariance) to control for body mass and length effects. Variables were log or log(x + 1) transformed. I tested for homogeneity of slopes, but body mass was the only parameter with significant slope differences. Therefore, I used a separate slope model for analysis of body mass and common slope models for all other variables. Shell growth and cage effect were tested using the species × cage interaction mean square for the error term. A repeated measures model ANOVA (analysis of variance) was selected for analysis of number of gametes because individual mussels were induced multiple times and sexes were analyzed separately. MINITAB release13 (MINITAB Inc., State College, Pa.) was used for all statistical tests. Comparisons were not significant at $p > 0.05$.

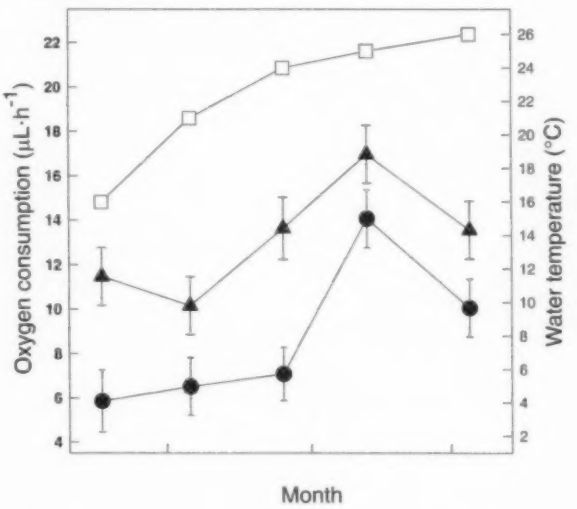
Results

Although the seasonal pattern of respiration was similar for each species, zebra mussels always had higher respiration rates than quagga mussels (Fig. 1; $F_{[1,171]} = 31.82$, $p < 0.0001$). Respiration for both species generally tracked the seasonal increase in water temperature. However, although significant for both species, the relationship of mass-standardized respiration and temperature was not strong (quagga mussels, $F_{[1,89]} = 13.30$, $p < 0.0001$, $r^2 = 0.130$, log(μL O_2·mg soft tissue mass^{-1} + 1) = 0.0106(temperature) – 0.0073; zebra mussels, $F_{[1,89]} = 11.65$, $r^2 = 0.116$, $p = 0.001$, log(μL O_2·mg soft tissue mass^{-1} + 1) = 0.0138(temperature) + 0.0653).

Quagga mussels were heavier than zebra mussels on most sampling dates (10/14, Fig. 2; $F_{[1,553]} = 6.49$, $p = 0.011$). Although body mass was lower in 1998 than in other years, quagga mussels were still heavier. Seasonal patterns for the 2 years with the most frequent sampling (1998 and 2000) were not similar. Both species' body mass remained relatively constant across the 1998 season; neither date nor the interaction of date and species had significant effects on body mass (date, $F_{[4,160]} = 0.29$; date × species, $F_{[4,160]} = 1.48$). In 2000, there was no difference between species ($F_{[4,247]} = 1.92$). Change in body mass with length was greater for quagga mussels than for zebra mussels on most dates (11/15, Table 2).

There was no difference in shell growth between cages ($F_{[2,2]} = 9.13$), and quagga mussels had greater shell growth than zebra mussels over the year ($F_{[1,2]} = 111.259$, $p = 0.009$). Growth of the mean-sized mussel (14.2 mm) was 5.70 (±0.22 standard error (SE)) for quagga mussels and 3.70 (±0.15 SE) mm for zebra mussels, which translates into shell growth rates of 14.8 and 9.6 μm·day^{-1} for quagga and zebra mussels, respectively.

Fig. 1. Mean (±1 standard error) oxygen consumption for Lake Erie zebra (*Dreissena polymorpha*, ▲) and quagga (*D. bugensis*, ●) mussels and ambient Lake Erie water temperature (□) during May–August 1998. Oxygen consumption for the mean-sized mussel (9.84 mg dry soft tissue body mass) was derived from analysis of covariance.



Smaller mussels grew more than did larger mussels, and growth decreased with size in both species. The decrease in growth with size was similar between species (quagga mussels, log(length added + 1) = 2.37 – 1.31(log(initial length + 1)), $F_{[1,132]} = 188.84$, $p < 0.0001$, $r^2 = 0.587$; zebra mussels, log(length added + 1)) = 2.09 – 1.2(log (initial length + 1)), $F_{[1,142]} = 116.80$, $p < 0.0001$, $r^2 = 0.451$).

Mussels were induced to spawn at various times during the season during different years. Indicators of the mussels' reproductive state can be inferred from readiness to spawn, measured as the percentage of mussels that spawned, and from the quantity of gametes released, measured by the mass of gametes released by mussels able to spawn. Although there are gaps in the data collection, a seasonal pattern in reproduction may be extrapolated by comparing years.

One indication of reproductive pattern is the percentage of mussels that will spawn when induced. The seasonal pattern

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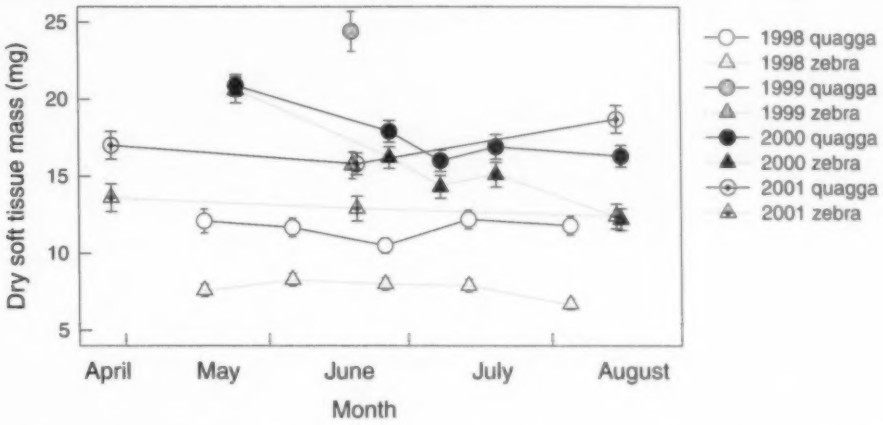
Fig. 2. Mean (±1 standard error) dry soft tissue body mass for Lake Erie zebra (*Dreissena polymorpha*) and quagga (*D. bugensis*) mussels during 1998–2001. Dry soft tissue body mass for the mean-sized mussel (17.74 mm shell length) was derived from analysis of covariance.



in the percentage of mussels that spawned was similar between species and sexes for each year (Fig. 3). The greatest difference in timing between species was in April 2001 when only quagga mussels released gametes. At that time, more males spawned than females. During the dates sampled there was an increase in ability to spawn during mid-June (1998, 1999, and 2001) or mid-July 2000.

Species differed in the mass of gametes released (Fig. 3; females, $F_{[1,150]} = 7.89$, $p = 0.006$; males, $F_{[1,114]} = 6.99$, $p = 0.009$). Although the species with the greatest output was not consistent, zebra mussels released more gametes on more dates than quagga mussels when differences in output were observed (Fig. 3; females: zebra mussel = 3/11, quagga mussel = 1/11; males: zebra mussel = 3/11, quagga mussel = 0). In addition, for all except zebra mussel males, the regression of mass of gametes and body mass were significant but the relationships were not strong (GM, log(gamete mass +1); BM, log(body mass +1); quagga mussel: females, GM = 0.345(BM) – 0.267, $F_{[1,92]} = 22.97$, $p < 0.0001$, $r^2 = 0.200$, males, GM = 0.380(BM) – 0.200, $F_{[1,90]} = 15.61$, $p < 0.0001$, $r^2 = 0.148$; zebra mussel: females, GM = 0.272(BM) – 0.089, $F_{[1,81]} = 7.06$, $p = 0.010$, $r^2 = 0.080$, males, GM = 0.044(BM) + 0.320, $F_{[1,58]} = 0.16$, $r^2 = 0.003$). The mass of gametes released was not correlated to the percentage of mussels that spawned for any group (Pearson's correlation coefficients: quagga mussel, females, $r = 0.239$, males, $r = 0.633$; zebra mussel, females, $r = 0.507$, males, $r = 0.583$).

The greatest difference in the percentage of mussels that spawned in 1999, when individual mussels were induced several times, occurred during the third induction for females and the last induction for males (Table 1). At both times more zebra mussels spawned. The percentage of mussels that spawned was not correlated to the number of gametes released for either sex of both species (Pearson's correlation coefficients: females, zebra mussel, $r = 0.679$, quagga mussel, $r = 0.601$; males, zebra mussel, $r = 0.649$, quagga mussel, $r = 0.431$).

Zebra mussels released more eggs than quagga mussels but there was no species difference in the number of sperm released (Table 3; Fig. 4). The interaction of collection event and species was significant in females, whereas only collection event was significant in males (Table 3). Mussels of both sexes for each species released gametes in the same pattern, and this pattern recurred with each induction. At each induction, mussels released the majority of gametes during the induction period and the number declined rapidly to zero by the third postinduction interval. Gamete release was highest during the first induction and decreased during subsequent inductions. Zebra mussels released a greater total number of eggs, but the number of sperm released did not differ between species (means ± SE for the mean-sized mussel (females = 28.5 mg body mass, males = 25.6 mg body mass) were derived from ANCOVA; females $F_{[1,32]} = 49.99$, $p < 0.0001$: zebra mussel, 56 624 ± 11 670, quagga mussel, 8074 ± 1361; males $F_{[1,26]} = 0.53$: zebra mussel, 151 008 ± 97 820, quagga mussel, 66 834 ± 73 609). Body mass had an effect on the total number of eggs ($F_{[1,32]} = 4.22$, $p = 0.048$) but not on the total number of sperm released ($F_{[1,26]} = 0.84$).

Discussion

There are significant differences in physiological energetics of zebra and quagga mussels. Furthermore, the pattern in physiological energetics provides an explanation for the displacement of zebra mussels by quagga mussels. Quagga mussels have lower respiration rates throughout the season. Lower respiration rates translate into lower energetic costs for quagga mussels and these lower costs leave more energy available that could be invested in growth or reproduction. However, there was little difference in reproduction between species. Zebra mussels, with higher respiration rates and smaller size, devote more to reproduction than to growth, whereas quagga mussels incorporate the excess energy imparted by lower costs into greater shell growth and body mass. Lower respiration rates coupled with greater shell growth and body mass are advantages for quagga mussels and are a likely explanation for their long-term ability to displace zebra mussels.

Respiration

Respiration in bivalves is influenced by temperature, food, and reproduction (Walz 1978*a*; Bayne and Newell 1983;

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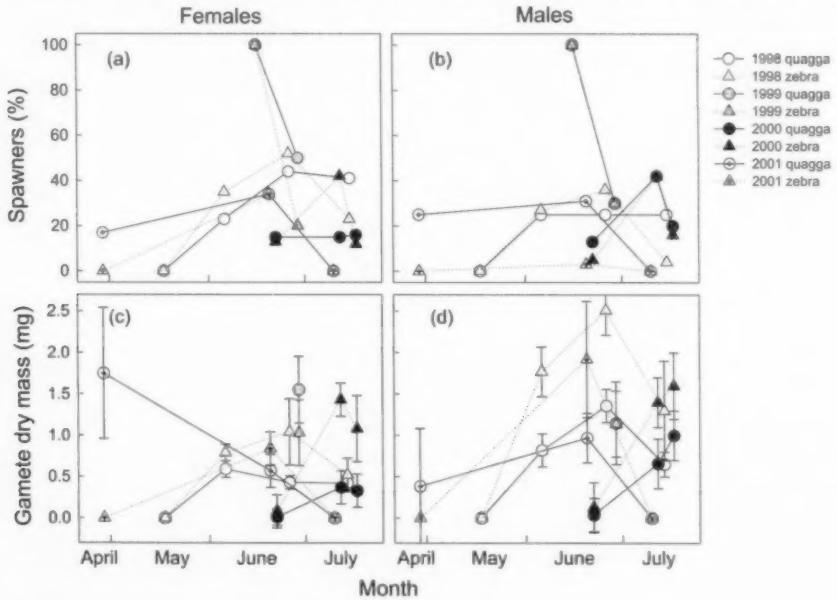
Table 2. Log(length) – log(body mass) regressions for Lake Erie zebra and quagga mussels on each sampling date in 1998–2001.

	Zebra mussels					Quagga mussels				
Date	*b* (SE)	Intercept (SE)	r^2	*n*	*F*	*b* (SE)	Intercept (SE)	r^2	*n*	*F*
1998										
17 May	2.09 (0.34)	–1.73 (0.42)	0.71	17	38.73	2.48 (0.14)	–2.01 (0.19)	0.95	17	305.84
5 June	1.68 (0.20)	–1.18 (0.20)	0.82	17	72.47	2.86 (0.17)	–2.50 (0.21)	0.95	17	287.95
25 June	2.64 (0.37)	–2.41 (0.46)	0.77	17	49.93	2.73 (0.12)	–2.40 (0.15)	0.97	17	545.91
13 July	1.78 (0.40)	–1.33 (0.51)	0.53	17	19.43	3.07 (0.21)	–2.75 (0.26)	0.93	17	223.80
4 August	1.86 (0.302)	–1.50 (0.37)	0.69	17	37.81	2.51 (0.16)	–2.06 (0.21)	0.93	17	233.12
1999										
18 June	1.82 (0.41)	–1.08 (0.50)	0.55	17	19.69	1.48 (0.45)	–0.47 (0.59)	0.33	23	10.83
2000										
24 May	1.75 (0.28)	–0.87 (0.35)	0.59	29	39.46	2.65 (0.09)	–1.99 (0.11)	0.95	40	886.32
26 June	2.47 (0.26)	–1.88 (0.33)	0.80	25	93.19	2.54 (0.09)	–1.92 (0.12)	0.97	28	762.52
7 July	2.04 (0.59)	–1.40 (0.74)	0.41	18	11.99	2.82 (0.11)	–2.31 (0.15)	0.96	28	618.28
19 July	3.38 (0.30)	–3.04 (0.36)	0.87	21	128.23	2.54 (0.09)	–1.94 (0.10)	0.97	25	864.65
15 August	2.38 (0.13)	–1.89 (0.17)	0.96	16	316.05	2.31 (0.15)	–1.67 (0.18)	0.91	24	244.12
2001										
27 April	1.66 (0.52)	–0.941 (0.66)	0.40	17	10.43	2.45 (0.14)	–1.83 (0.17)	0.95	19	308.54
19 June	2.49 (0.33)	–2.00 (0.42)	0.80	16	58.09	2.52 (0.11)	–1.95 (0.14)	0.96	24	521.46
14 August	2.50 (0.37)	–2.02 (0.47)	0.81	16	45.63	2.34 (0.11)	–1.65 (0.14)	0.95	24	476.22

Note: Regressions for both species were significant (zebra mussels: 7 July 2000, $p = 0.003$; 27 April 2001, $p = 0.005$; quagga mussels: 18 June 1999, $p = 0.003$; both species, all other dates: $p < 0.0001$). *b*, slope; SE, standard error; *n* = sample size.

Fig. 3. (*a*, *b*) Percentage of Lake Erie zebra (*Dreissena polymorpha*) and quagga (*D. bugensis*) mussels that spawned when induced during 1998–2001. (*c*, *d*) Mean (±1 standard error) gamete dry mass for zebra and quagga mussels induced to spawn during 1998–2001. Gamete dry mass for the mean-sized mussel (females = 18.41 mg, males = 19.28 mg) was derived from analysis of covariance.



Sprung 1995*a*). Quagga mussels are more susceptible to high water temperatures than are zebra mussels (Domm et al. 1993; Spidle et al. 1995; Karatayev et al. 1998). However, although quagga mussels were initially found primarily in deeper water, their distribution now overlaps with that of zebra mussels, extending into shallow water (Mills et al. 1999) and warm water plumes (Mitchell et al. 1996). During this study, water temperature at this western basin site reached 26°C. Although respiration rates of both species tracked the seasonal increase in water temperature, the relationship of mass-standardized respiration rates and temperature was significant, albeit weak. The upper thermal limit of quagga mussels is lower than that of zebra mussels (Domm et al. 1993; Spidle et al. 1995), and although respiration rates of

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Table 3. Analysis of variance results for number of gametes.

Source of variation	df	MS	*F*	*p*
Females				
Collection event[a]	8	210 787	3.11	NS
Species[a]	1	535 689	7.90	0.0228
Collection event × species[b]	8	67 766	3.94	0.0002
Males				
Collection event[b]	7[c]	25 620 509	11.70	0.0001
Species[b]	1	5 287 700	2.41	NS
Collection event × species[b]	7	3 920 327	1.79	NS

Note: Collection event is either the induction or postinduction event; NS, not significant; df, degrees of freedom; MS, mean square.

[a]Error term = collection event × species.

[b]Error term = subject(collection event × species); females, df = 297; males, df = 216.

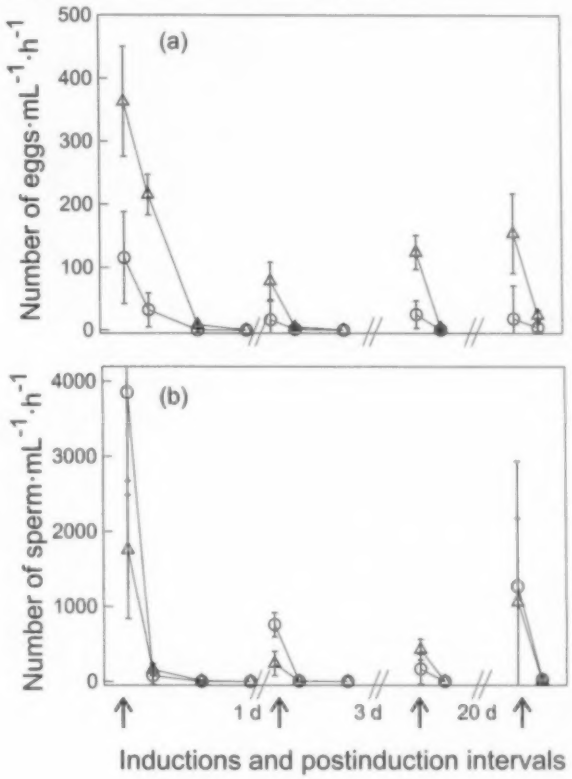
[c]One gamete collection event was not included in the analysis because no males spawned.

quagga mussels were lower than those for zebra mussels throughout the season, the difference between the rates decreased somewhat after summer lake water temperatures exceeded 24°C. It may be that as water temperatures approach their upper limit, quagga mussels may increase their respiration rates more than zebra mussels. Nonetheless, lake water temperatures reached 26°C during this study and quagga mussels maintained their lower respiration rates throughout seasonal changes in water temperature, indicating their ability to tolerate warm water habitats.

Respiration in bivalves is associated with feeding (Bayne and Newell 1983) and increases with feeding activity, ration, clearance, ingestion, and the handling and processing of food (Bayne et al. 1989). Zebra mussels are typical bivalves and respiration rates increase with food concentration (Madon et al. 1998; Stoeckmann and Garton 2001), are correlated to increased ingestion at those concentrations (Madon et al. 1998), and indicate costs associated with food handling and processing (Madon et al. 1998). Zebra and quagga mussel clearance rates of *Chlorella* do not differ (Ackerman 1999). However, the species may differ in their clearance rates of natural seston. Although the mussels in this study experienced the same food conditions, the influence of feeding and food conditions on respiration may differ between species and may be responsible for the differences in respiration rates observed in this study.

When food quality or turbidity conditions are less than optimal, lower respiration rates would be an advantage for quagga mussels by decreasing energetic demands. Inorganic sediment decreases food quality and poor food quality has negative effects on clearance, ingestion, absorption, and assimilation (Madon et al. 1998) and ultimately decreases growth in zebra mussels (Madon et al. 1998; Stoeckmann and Garton 2001). When experimental levels of turbidity were combined with temperature (15 and 25°C, within the seasonal range of this study), Summers et al. (1996) found no difference in respiration between zebra and quagga mussels. However, increased turbidity decreased respiration rates and the decrease was more pronounced in quagga mussels (Summers et al. 1996). The replacement of zebra mussels by quagga mussels in Ukraine reservoirs has been linked to higher tolerance of quagga mussels to silt and low oxygen conditions (Karatayev et al. 1998). Increased respiration rates

Fig. 4. Mean (±1 standard error) number of (*a*) eggs and (*b*) sperm released by individually marked Lake Erie zebra (*Dreissena polymorpha*, △) and quagga (*D. bugensis*, ○) mussels induced four times (↑) at intervals of 1, 3, and 20 days (d) after the previous induction during June–July 1999.



in zebra mussels at high levels of sediment, coupled with low clearance rates (Madon et al. 1998), may be more energetically stressful for zebra mussels than for quagga mussels and implies that zebra mussels may not tolerate high sediment conditions. Turbidity was not measured in this study but lower respiration rates would be advantageous, allowing quagga mussels to decrease energy demands at higher sediment levels, thereby increasing energy available for growth or reproduction.

Reproduction, both gametogenesis and spawning, influence metabolic costs in mussels (Bayne and Newell 1983; Sprung 1991). In zebra mussels, respiration rates are greater during the reproductive period than at other times of the year (Lyashenko and Karchenko 1989) and seasonal variation in metabolic costs is linked to reproductive status (Stoeckmann and Garton 1997). Although there was little difference between species in most reproductive measures, body mass of zebra mussels is lower than that of quagga mussels, thus zebra mussels devote a greater proportion of body tissue to reproduction than do quagga mussels. Higher respiration rates in zebra mussels may reflect the support of this additional reproductive tissue. The influence of reproduction on respiration may be responsible for the differences observed in respiration rates between species.

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Growth and reproduction

Quagga mussels grew in shell length faster than did zebra mussels. Differences in the species' growth rates may begin as early as the larval stage (Martel et al. 2001); quagga mussels settle and metamorphosize at a larger shell size than do zebra mussels and therefore either larval growth is faster or quagga mussels spend more time in the plankton (Wright et al. 1996; Martel et al. 2001). In the benthic population, quagga mussels are generally larger than zebra mussels and constitute a larger proportion of the dreissenid biomass, and these differences increase as the time that they occupy an area increases (Mills et al. 1999; Jarvis et al. 2000). Daily shell growth rates in this study were lower than summer growth rates measured on zebra mussels from the same location (Stoeckmann and Garton 1997), in a different lake (Garton and Johnson 2000), and for zebra and quagga mussels in a transplant experiment (MacIsaac 1994). However, growth rates in this study were averaged over 1 year. Shell growth stops or slows in the winter (Walz 1978*b*; Sprung 1995*b*; Allen et al. 1999), thus shell growth rates averaged over 1 year and including winter growth, as in this study, would be lower.

In addition to greater shell growth, quagga mussels were heavier than zebra mussels. Soft tissue mass was measured at various times during the spring and summer over 4 years and the differences in body mass between species were consistent. Zebra and quagga mussels' shell shapes differ (Domm et al. 1993). Quagga mussel shells are broader than zebra mussel shells, and this difference likely contributes to the difference in body mass. In a reciprocal transplantation experiment, although there was no difference between species in length and mass-specific growth rates of tissue and shell mass combined, the percent change in mass of quagga mussels was greater than that of zebra mussels (MacIsaac 1994). Poor food quality and stressful conditions decrease growth in zebra mussels (Madon et al. 1998; Stoeckmann and Garton 2001). However, the effect of experimentally manipulated turbidity and temperature on shell growth of zebra and quagga mussels was inconclusive (Thorp et al. 1998).

Greater body mass in quagga mussels could represent more reproductive tissue if quagga mussels reproduce as zebra mussels typically do, increasing fecundity with body size (Walz 1978*c*; Sprung 1995*b*). However, many of the reproductive components measured for mussels induced during the season and when individual mussels were induced several times were similar between species; there was no difference between species in the percentage of individuals capable of spawning or the number of sperm released by individuals, but species differed in the mass of gametes released and the number of eggs. Although larger mussels did increase the mass of gametes released slightly, these relationships were not strong. However, the number of eggs increased with body mass, but only in zebra mussels. When mussels of the same size were compared, the combination of similar or greater reproduction and smaller body mass indicated that zebra mussels devote a greater proportion of body tissue to reproduction than do quagga mussels.

The greatest difference in individual spawning occurred in females, with zebra mussels releasing more eggs than quagga mussels. Results of these multiple inductions of individual mussels are consistent with trends for zebra mussel females (Walz 1978*c*). Although the time periods used were not specified, Walz (1978*b*) also found that the most eggs were released and the highest percentage of mussels spawned with the first induction, the percentage of mussels that spawned and the number of eggs released decreased with subsequent inductions, and the number of eggs increased with an increased interval between inductions. In addition, the average number of eggs released by female zebra mussels in this study was similar to that reported by Walz (1978*b*).

The largest difference in reproductive pattern was quagga mussels' ability to spawn much earlier in the season than zebra mussels. When induced at 9°C in April, quagga mussels spawned, whereas zebra mussels did not. April spawning is well before the typical spawning pattern of zebra mussels at this site (Garton and Haag 1993), and 9°C is below the 12°C considered the minimum temperature for maturation of gametes in zebra mussels (Sprung 1987). The influence of temperature on reproduction must differ for quagga mussels. Female quagga mussels from deepwater sites had mature eggs at 4.8°C (Roe and MacIsaac 1997) and spawned at 9°C in a transplant experiment (Claxton and Mackie 1998), but in the same study, no zebra mussels matured gametes when transplanted to the hypolimnion where temperatures were between 4 and 9°C (Claxton and Mackie 1998). Although early spawning was examined only during the last year of this study and histological data would confirm these findings, results show that quagga mussels in shallow water mature gametes and are capable of spawning earlier than are zebra mussels. This evidence also supports the sighting of veligers in early to mid-May (John Hageman, Ohio State University, F.T. Stone Laboratory, Put-In-Bay, OH 43456, personal communication).

The lack of correlation between reproduction and size may be related to the timing of gamete collections and the age and size distribution of the study population. One of the largest differences in reproduction was earlier spawning in quagga mussels. Although there was little difference at other times, timing of collections may not have included the total period that mussels were capable of spawning. Age and size distribution in the population also may have influenced the results. Quagga mussels are typically larger than zebra mussels, especially in populations where they have been present for a longer time than at this site (Mills et al. 1999; Jarvis et al. 2000). The quagga mussels used represented the size range in the study population, and the maximum length included was 31 mm. However, quagga mussels may exceed 40 mm in some populations (Jarvis et al. 2000). The lack of difference in reproduction between species and a strong correlation between reproduction and size may indicate that quagga mussels in this Lake Erie population have not yet reached their maximum size, and thus their maximum reproductive output.

Advantage: quagga mussels

Lower respiration rates are an important factor responsible for greater body mass and shell growth in quagga mussels. Metabolic costs compose a significant portion of the seasonal energy budget for zebra mussels (90%) and are the most influ-

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ential factor in their energy allocation (Stoeckmann and Garton 1997). Lower respiration rates decrease energetic costs for quagga mussels and leave more energy available for growth and reproduction. Reproduction, comparable to that of zebra mussels, coupled with greater body mass implies that quagga mussels invest a greater proportion of excess energy into growth. Body mass not devoted to reproductive tissue must represent energy reserves. By investing in reserves, quagga mussels may be better able to withstand and survive stressful midsummer periods of high water temperatures coupled with low food availability. Conversely, zebra mussels devote a greater proportion of body tissue to reproduction than do quagga mussels. Higher respiration rate during stressful times and potentially exacerbated by depleted postspawning body condition leaves zebra mussels less able to withstand stressful midsummer conditions, resulting in death.

Zebra mussels may be more of an *r* strategist in their life history than are quagga mussels. They appear to emphasize reproduction, breeding early, often, and producing many gametes and, as a result, have lower growth and earlier death. These characteristics may make zebra mussels better invaders with wide dispersal, faster population growth rate, and a greater potential to spread and exploit new habitats. A life history pattern of this sort agrees with the observed invasion pattern and current distribution of both species.

Lower respiration rate allows greater growth and ultimately survival of quagga mussels and is likely the advantage responsible for their displacement of zebra mussels. Spread of quagga mussels and displacement of zebra mussels will continue throughout the area of sympatry. However, quagga mussels with their lower metabolic scope cannot tolerate the same temperature regime as zebra mussels (also noted in lower spawning temperature). Thermal tolerance differences may ultimately provide a gradient in distribution of the two species in North America.

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The relation between age-0 rainbow trout (*Oncorhynchus mykiss*) abundance and winter discharge in a regulated river

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Abstract: We identified and experimentally tested a discharge–abundance relation that predicted, based on the mean river discharge in the second half of winter (15 January – 31 March), the spring abundance of age-0 rainbow trout (*Oncorhynchus mykiss*) in a section of the Henrys Fork of the Snake River, Idaho, with complex bank habitat. We also considered a competing hypothesis in which autumn abundance determined spring abundance. We established that large abundances of age-0 trout were present in autumn (34 000 – 81 000) and lower abundances remained in spring (8000 – 15 000). Winter loss of age-0 trout was initiated in January. Spring abundance in 1996–1998 was related to autumn abundance ($r^2 > 0.99$) and mean discharge in the second half of winter (17.1–22.8 $m^3 \cdot s^{-1}$; $r^2 > 0.99$) but not mean discharge in the first half of winter (15.1–21.1 $m^3 \cdot s^{-1}$; $r^2 = 0.11$). We experimentally maintained a high discharge (20–21 $m^3 \cdot s^{-1}$) in the second half of winter in 1999 to test model predictions. Autumn abundance failed to predict spring abundance (observed = 11 109; predicted = 6822; 95% prediction interval = 4669–8975). However, the discharge–abundance model accurately predicted spring abundance (predicted = 11 980; 95% prediction interval = 10 728 – 13 231). Higher discharge in the second half of winter may have provided more bank habitat at a critical time for survival.

Résumé : Nous avons découvert et vérifié expérimentalement une relation entre le débit et l'abondance qui prédit, d'après le débit moyen de la rivière durant la seconde moitié de l'hiver (15 janvier – 31 mars), l'abondance des truites arc-en-ciel (*Oncorhynchus mykiss*) d'âge 0 au printemps dans un secteur à habitats de berge complexes dans le tributaire the Henrys Fork de la rivière Snake en Idaho. Nous avons aussi examiné une hypothèse de rechange qui relie l'abondance au printemps à l'abondance à l'automne. Les abondances de truites d'âge 0 sont fortes à l'automne (34 000 – 81 000) et plus faibles au printemps (8000 – 15 000). La perte de truites d'âge 0 commence en janvier. L'abondance au printemps en 1996–1998 était fonction de l'abondance à l'automne ($r^2 > 0{,}99$) et du débit moyen dans la seconde moitié (17,1–22,8 $m^3 \cdot s^{-1}$; $r^2 > 0{,}99$), mais pas dans la première moitié (15,1–21,1 $m^3 \cdot s^{-1}$; $r^2 = 0{,}11$) de l'hiver. Nous avons maintenu expérimentalement un débit élevé (20–21 $m^3 \cdot s^{-1}$) pendant la seconde moitié de l'hiver en 1999 pour vérifier les prédictions du modèle. L'abondance en automne n'a pas permis de prédire l'abondance au printemps (observée = 11 109; prédite = 6822; intervalle de prédiction 95 % = 4669–8975). En revanche, le modèle basé sur le débit et l'abondance a prédit de façon précise l'abondance au printemps (prédite = 11 980; intervalle de prédiction 95 % = 10 728 – 13 231). Le fort débit durant la seconde moitié de l'hiver accroît probablement les habitats de berge à un moment critique pour la survie.

[Traduit par la Rédaction]

Introduction

In a study of rainbow trout (*Oncorhynchus mykiss*) recruitment in the Henrys Fork of the Snake River, Idaho, Mitro and Zale (2002*a*) investigated when apparent mortality of age-0 trout occurred seasonally and where recruitment occurred in a 25-km reach of the river system. They found evidence that availability of winter habitat limited rainbow trout recruitment in the Henrys Fork. Most river sections in the Henrys Fork had only simple bank habitat and did not support age-0 rainbow trout throughout winter (Mitro and Zale 2002*a*). The winter habitat that supported age-0 trout was complex bank habitat, and age-0 trout survived throughout winter only where such habitat was present, primarily in the Box Canyon

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river section. Other studies have identified salmonid recruitment limitation in association with limited winter habitat availability (Elliott 1994; Cunjak 1996; Cunjak et al. 1998).

Interannual variation in first-winter apparent survival in the Box Canyon river section of the Henrys Fork was relatively low (18–23%; Mitro and Zale 2002*a*) compared with interannual variation in winter survival of salmonids in other river systems (Seelbach 1993; Ward and Slaney 1993; Quinn and Peterson 1996). However, there was interannual variability in recruitment from Box Canyon. Understanding the mechanism behind any variation in recruitment is important to fisheries managers because such knowledge may help guide management options that may improve a fishery.

We formulated and tested two hypotheses regarding what factors influenced or determined annual differences in spring abundance of age-0 rainbow trout in the Box Canyon section of the Henrys Fork. One hypothesis was that abundance in spring was a function of abundance in the previous summer or autumn, i.e., the more age-0 trout entering a winter, the more that survive. The second hypothesis was that abundance in spring was a function of river discharge, i.e., different discharge levels differentially inundated complex bank habitat in Box Canyon, thereby influencing the availability of winter habitat and the abundance of age-0 trout in spring. We investigated these hypotheses using data from Mitro and Zale (2002*a*) and tested the hypotheses using additional data collected in winter 1998–1999 when we manipulated discharge from Island Park Dam into the river.

Materials and methods

Study area

The Henrys Fork of the Snake River at Island Park Dam (44°24′59″ latitude, 111°23′41″ longitude) is at an elevation of 1897 m and has a drainage area of 1246 km^2. The mean annual discharge through Island Park Dam from October 1994 through April 1999 was 23 $m^3 \cdot s^{-1}$ (range 5.9–78.4 $m^3 \cdot s^{-1}$). The Buffalo River enters the Henrys Fork about 0.25 km downstream of Island Park Dam. The Buffalo River is a spring-fed river that has a relatively constant discharge of about 6 $m^3 \cdot s^{-1}$.

Box Canyon begins at the confluence of the Henrys Fork and the Buffalo River and is 4 km long with a mean width of 70 m. (See fig. 1 in Mitro and Zale (2002*a*) for a map of the study area.) Box Canyon is a relatively high gradient area (0.45%) with a cobble–boulder substrate and sloping banks (20–45°) strewn with boulders, large cobbles, and large woody debris. This river section has complex bank habitat consisting of rocks and woody debris; there are few macrophytes across the channel. Most successful overwintering of age-0 rainbow trout occurs in this section (Mitro and Zale 2002*a*). Box Canyon was divided into two sections for the purpose of estimating abundance: upper Box Canyon (1.5 km) and lower Box Canyon (2.5 km). Upper Box Canyon is characterized by areas of rapids, depths exceeding 1 m, and large uneven substrate. Lower Box Canyon is wider and the depth is usually less than 1 m. Generally, no ice forms in Box Canyon. Winter water temperature is moderated by hypolimnetic releases from Island Park Reservoir (2–4°C) and water from the spring-fed Buffalo River (1–6°C).

Last Chance is immediately downstream of Box Canyon and is 4 km long with a mean width of 95 m. Last Chance is a moderate gradient area (0.3%) with a cobble substrate and vertical consolidated sand and silt banks held together by wet meadow grasses and sedges. The channel depth is usually less than 1 m and there are extensive macrophyte beds across the channel throughout the river section. Bank habitat in Last Chance is simple, lacking the rocks and woody debris prevalent upstream in Box Canyon. Macrophyte beds decrease through winter (but are not eliminated) because of senescence and grazing by trumpeter swans (*Cygnus buccinator*) and other waterfowl (Van Kirk and Martin 2000). Generally no ice forms in Last Chance and none was observed during this study.

Age-0 rainbow trout abundance and discharge

We estimated the abundance of age-0 trout in autumn (October) and spring (May) using mark–recapture and removal methodologies (Mitro and Zale 2000, 2002*a*, 2002*b*). We sampled two areas in autumn in lower Box Canyon (1995–1998) using mark–recapture to estimate abundance (Mitro and Zale 2002*b*). Mark–recapture sample areas were 100 m long and extended from bank to bank. We used the same sample areas each year. We collected age-0 rainbow trout by wading with boat-mounted electrofishing gear (continuous DC, 250 V) from one bank to the other along eight transects per sample area, perpendicular to the flow. Each sample area was sampled either 4 or 5 days, generally every other day. Trout were marked with partial fin clips and a different fin clip was used on each day. Sample areas were considered closed such that no significant losses or additions occurred during the sampling period (Mitro and Zale 2002*b*). Mark–recapture data were analyzed using the Chao M_t estimator in program CAPTURE (Chao 1989; Rexstad and Burnham 1991; Mitro and Zale 2002*b*). Mean abundance estimates for sample areas were extrapolated to areas not sampled to estimate the total abundance of age-0 trout in each river section. Confidence intervals (95%) for estimates of total abundance included within-sample area, among-sample area, and extrapolation error. See Mitro and Zale (2002*a*, 2002*b*) for further details on the sampling procedure and data analysis.

We sampled multiple 10- to 15-m bank units along the banks in upper Box Canyon in autumn (1995–1998) and throughout Box Canyon in spring (1996–1999) using removal methodologies to estimate abundance (Mitro and Zale 2000, 2002*a*). Bank units were sampled primarily by three-pass removal (about 10% by single-pass removal) by wading with a handheld electrode (continuous DC, 250 V). We sampled seven bank units in upper Box Canyon in autumn in 1995 and 10 bank units in 1996–1998. We sampled 20 bank units in Box Canyon in spring in 1996 and 50 bank units in 1997–1999. Three-pass removal data were analyzed using the Zippin maximum likelihood removal estimator (Zippin 1956; Otis et al. 1978; Rexstad and Burnham 1991). Single-pass removal data were analyzed using a mean capture probability model calibrated for the Henrys Fork (Mitro and Zale 2000). Mean abundance estimates for bank units were extrapolated to areas not sampled to estimate the total abundance of age-0 trout in each river section.

We identified the temporal pattern of overwinter loss of age-0 rainbow trout from Last Chance using a catch-per-

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unit-effort methodology. Last Chance was used as a surrogate for Box Canyon because Box Canyon is inaccessible during winter. We assumed that, in general, temporal shifts in habitat use and abundance would be similar in the two sections. Smith and Griffith (1994), in a study of first-year survival of caged age-0 rainbow trout in the Box Canyon and Last Chance sections of the Henrys Fork, found that the timing of mortality is independent of river location. Ten random bank-to-bank transects were sampled by electrofishing (continuous DC, 250 V) once a month from November through April in winters 1996–1997, 1997–1998, and 1998–1999.

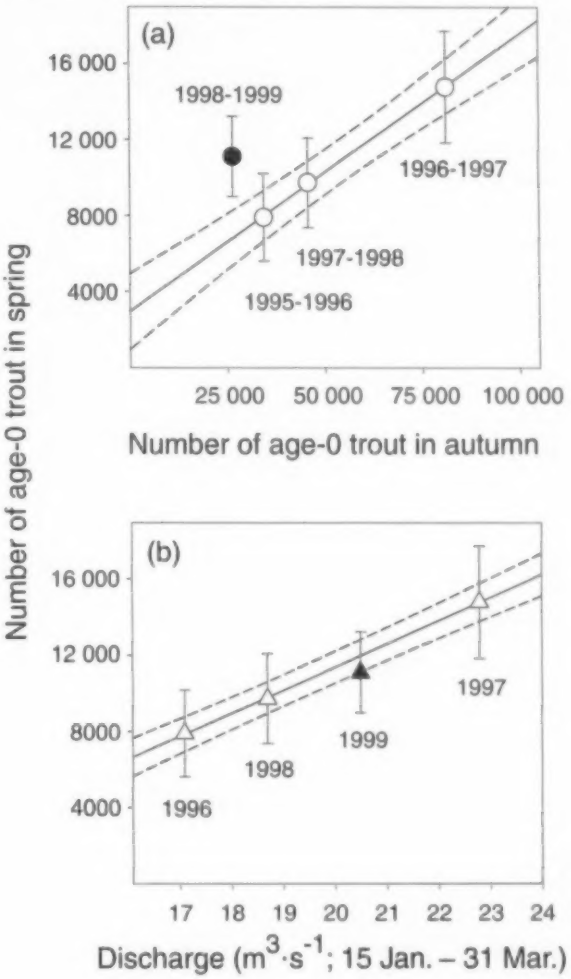
We used simple linear regression to quantify the relation between autumn and spring age-0 rainbow trout abundance and between discharge during the first (1 November – 14 January) and second (15 January – 31 March) halves of winter and spring age-0 trout abundance using data from the first 3 years of the study. Discharge data for the Henrys Fork were obtained for each winter from the United States Geological Survey gauging station near Island Park Dam (Station 13042500). Discharge during the second half of winter 1998–1999 (the 4th year of the study) was maintained at a relatively high level (20–21 $m^3 \cdot s^{-1}$) to experimentally test the discharge–abundance model. Each model was tested by comparing the number of age-0 rainbow trout in Box Canyon in spring 1999 to the model prediction.

Results

Large abundances of age-0 rainbow trout were present in Box Canyon in autumn in each year of the study: 34 353 in 1995 (95% confidence interval (CI) = 29 781 – 38 927), 81 165 in 1996 (95% CI = 61 858 – 100 471), and 45 723 in 1997 (95% CI = 37 335 – 54 110). Considerable losses (attributable to mortality or movement) of age-0 trout occurred during each winter. The temporal pattern of age-0 trout loss as measured in Last Chance was consistent among years. There was no evidence of loss in November or December, the loss was initiated between December and January and continued through March, and numbers then increased in April. The total catch per 10 transects by month was 139, 146, 64, 28, 15, and 33 for November 1996 – April 1997 and 148, 151, 72, 7, 4, and 55 for November 1997 – April 1998. The abundance of age-0 rainbow trout in Box Canyon in spring was 7903 in 1996 (95% CI = 5608 – 10 197), 14 788 in 1997 (95% CI = 11 835 – 17 740), and 9730 in 1998 (95% CI = 7372 – 12 082).

There was a positive relation between the abundance of age-0 rainbow trout in autumn and spring (Fig. 1*a*; intercept = 2958 and slope = 0.146; $r^2 > 0.99$) and a positive relation between discharge in the second half of winter and spring age-0 trout abundance (Fig. 1*b*; intercept = –12 887 and slope = 1213; $r^2 > 0.99$) for the first 3 years of this study. Winter discharge varied within and among years. Mean (and minimum) discharge in the first half of winter (1 November – 14 January) was 15.6 (14.7) $m^3 \cdot s^{-1}$ in 1995–1996, 15.1 (13.6) $m^3 \cdot s^{-1}$ in 1996–1997, and 21.1 (18.4) $m^3 \cdot s^{-1}$ in 1997–1998. In the second half of winter (15 January – 31 March), mean (and minimum) discharge was 17.1 (14.2) $m^3 \cdot s^{-1}$ in 1996, 22.8 (17.7) $m^3 \cdot s^{-1}$ in 1997, and 18.7 (15.8) $m^3 \cdot s^{-1}$ in 1998. The number of age-0 trout in Box Canyon in spring was positively related to discharge in the second half of winter ($r^2 > 0.99$; Fig. 1*b*) but not the first half of winter (r^2 = 0.11).

Fig. 1. Relation between (*a*) age-0 rainbow trout (*Oncorhynchus mykiss*) abundance in autumn and (*b*) mean discharge ($m^3 \cdot s^{-1}$) from Island Park Dam between 15 January and 31 March and abundance of age-0 trout in spring in Box Canyon. Each model was fitted to data from 1996–1998 (open symbols) and tested with an observation from 1999 (solid symbol). Solid line represents the linear regression line; broken lines represent the 95% prediction intervals; error bars represent the 95% confidence intervals.



Discharge was experimentally maintained at a relatively high mean level during the second half of winter 1998–1999 at 20.5 $m^3 \cdot s^{-1}$ (minimum = 17.2 $m^3 \cdot s^{-1}$). Age-0 rainbow trout abundance in Box Canyon and the temporal pattern of loss as measured in Last Chance during that winter were consistent with observations from the previous three winters (Fig. 1*b*). A large abundance of age-0 rainbow trout was in Box Canyon in autumn 1998: 26 460 (95% CI = 18 654 – 34 266). The total catch per 10 transects in Last Chance by

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month was 132, 105, 52, 17, 12, and 28 for November 1998 – April 1999. In spring 1999, the abundance of age-0 trout in Box Canyon was 11 109 (95% CI = 8 986 –13 233).

The model relating abundance in autumn and spring failed to predict the number of age-0 rainbow trout in Box Canyon in spring 1999. This model predicted that with 26 460 age-0 trout present in autumn, there would be 6822 age-0 trout in spring. This prediction was about 39% less than the empirical estimate of abundance in spring; the 95% prediction interval of 4669–8975 failed to capture the empirical estimate of 11 109.

The discharge–abundance model accurately predicted the number of age-0 rainbow trout in Box Canyon in spring 1999 based on the mean discharge during the second half of winter. The model predicted that at a mean discharge of 20.5 $m^3 \cdot s^{-1}$ observed for 15 January – 31 March 1999, there would remain 11 980 age-0 trout in Box Canyon in spring. This prediction was about 8% greater than the empirical estimate of abundance in spring; the empirical estimate of 11 109 was within the 95% prediction interval of 10 728 – 13 231.

Discussion

We tested whether autumn abundance or discharge in the second half of winter was a better predictor of spring abundance of age-0 rainbow trout in the Box Canyon section of the Henrys Fork. Spring abundance of age-0 trout was related to both autumn abundance and discharge in the first 3 years of the study. However, in testing the models with additional data from 1998–1999, only the discharge–abundance model accurately predicted spring age-0 trout abundance. Mitro and Zale (2002*a*) showed that complex bank habitat could be limiting to age-0 rainbow trout during winter in a sense that trout were present in spring only where such habitat was present and not where it was absent. This study showed that varying discharge, and hence the amount of winter habitat, at a time when habitat availability was critical to survival influenced spring abundance.

The number of age-0 rainbow trout in Box Canyon in spring was positively related to discharge during the second half of winter; there was no relation between spring abundance and discharge during the first half of winter. The catch-per-unit-effort data from Last Chance indicated that the loss of age-0 trout, which likely included movement, occurred in midwinter. Higher discharge in the second half of winter may therefore have provided more bank habitat in Box Canyon at a critical time for survival. Bank habitat that provides interstitial space for shelter is critical to the winter survival of age-0 river salmonids (Griffith and Smith 1993; Cunjak 1996; Mäki-Petäys et al. 1997). Trout from other river sections may move upstream to find available bank habitat (Mitro and Zale 2002*a*) as macrophytes become unsuitable for winter survival and trout begin to move to bank habitat (Griffith and Smith 1995).

The positive relation between age-0 trout abundance in Box Canyon in autumn and spring in the first 3 years of this study suggested that perhaps discharge was not such an important variable. However, the number of age-0 trout in autumn 1998 was lower than in any other year of this study and the number of age-0 trout in spring 1999 was the second largest. The failure of autumn abundance to predict spring abundance suggested that discharge during the second half of winter, that is, habitat availability, rather than production was the driving factor in determining spring abundance of age-0 rainbow trout.

An increase in the number of age-0 rainbow trout captured in 10 random transects in Last Chance occurred in April each year. This increase occurred among trout using center channel habitat (Mitro and Zale 2002*a*) and suggested that age-0 trout were moving back into Last Chance at the end of winter. These trout were probably not concealed in the substrate earlier in the winter because the substrate in Last Chance is highly embedded. The movement of age-0 trout back to center channel habitat in April suggests that concealment substrate is no longer critical at that time.

A positive relation between the mean discharge in February and the survival of age-0 Atlantic salmon (*Salmo salar*) was observed in New Brunswick and Newfoundland (Gibson and Meyers 1988). A positive relation was also found between winter discharge and age-0 Atlantic salmon survival in Catamaran Brook, N.B. (Cunjak et al. 1998). Unlike these streams, the Henrys Fork is a regulated river. Discharge can be controlled and used as a management tool to improve natural recruitment of rainbow trout in the Henrys Fork. Applicability of our findings elsewhere is unknown but deserves evaluation, particularly in other tailwater systems and perhaps also streams subjected to artificial reductions in discharge during winter such as is associated with snowmaking at ski areas.

If discharge is increased to support age-0 trout during the second half of winter in the Henrys Fork, any increase in discharge should precede or coincide with the midwinter loss of age-0 trout. In this study, with mean discharge in the first half of winter ranging from 15.1 to 21.1 $m^3 \cdot s^{-1}$, the loss of age-0 trout was initiated between December and January. However, when discharge was relatively low in winter 1994–1995 (mean 7.2 $m^3 \cdot s^{-1}$), the loss was initiated between November and December (Mitro 1999). Discharge and the temporal pattern of age-0 trout loss should therefore be monitored to assist decision-making about discharge regulation.

We recommend a high level of discharge (>20 $m^3 \cdot s^{-1}$) during the second half of winter to improve the recruitment of age-0 rainbow trout in the Henrys Fork. The water stored in Island Park Reservoir is currently managed for multiple uses, including power production and irrigation. In past winters, excess water has been released from the reservoir in early winter in anticipation of a large snowpack. Delay of such releases until late winter when age-0 rainbow trout move from midstream macrophytes to bank cover would enhance spring abundances of age-0 trout in Box Canyon. We also recommend continued testing of the discharge–abundance relation, particularly beyond the bounds of discharge encountered in this study.

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Explaining diet composition of North Sea cod (*Gadus morhua*): prey size preference vs. prey availability

Jens Floeter and Axel Temming

Abstract: The nature and significance of size preference for fish prey in the diet selection of North Sea cod (*Gadus morhua* L.) was analysed. The analysis combined information on size-specific abundance derived from bottom trawl surveys with prey size frequencies in cod stomachs from the International North Sea Stomach Database. To estimate the abundance of all potential fish prey in the sea, a length-based number spectrum was calculated, corrected for gear efficiency by the application of a species-specific correction factor, and weighted by local predator abundance to take the spatial–temporal overlap between cod and its prey into consideration. A prey size preference model for cod feeding on fish is presented. Results showed that the preferred predator-to-prey weight ratio is an exponentially increasing function of predator size and an exponentially decreasing function of the slope of the number spectrum. More than 75% of fish found in the stomachs of North Sea cod originated from the least preferred quartile of the prey size range, indicating that prey abundance is the main determinant of the diet composition.

Résumé : Nous avons analysé la nature et l'importance de la préférence de tailles chez les poissons proies dans la sélection alimentaire de la morue franche (*Gadus morhua* L.) de la Mer du Nord. Notre analyse combine des renseignements sur l'abondance en fonction de la taille provenant d'inventaires au chalut de fond et des fréquences de tailles de proies dans les estomacs de morues obtenues de la banque de données « International North Sea Stomach Database ». Pour estimer l'abondance de tous les poissons proies potentiels dans la mer, nous avons calculé un spectre des nombres en fonction de la longueur que nous avons corrigé pour tenir compte de l'efficacité des engins de récolte à l'aide d'un facteur de correction particulier pour chaque espèce; nous l'avons aussi pondéré en fonction de l'abondance locale des prédateurs pour tenir compte du chevauchement spatio-temporel de la morue et de ses proies. Nous présentons un modèle de préférence des tailles de proies applicable aux morues piscivores. Le modèle montre que le rapport préféré des masses prédateur–proie est une fonction exponentielle qui croît avec la taille du prédateur et qui décroît avec la pente du spectre des nombres. Plus de 75 % des poissons retrouvés dans les estomacs des morues de la Mer du Nord se retrouvent dans le quartile d'étendue des tailles de proies les moins recherchées, ce qui indique que l'abondance des proies est le facteur déterminant principal de la composition du régime alimentaire.

[Traduit par la Rédaction]

Introduction

Trophic interactions in aquatic ecosystems are determined by the size of predators and their prey rather than by their ages. However, fish population models in boreal and temperate regions are generally age-based. When the North Sea fishery assessment advanced to the multispecies virtual population analysis (MSVPA; Helgason and Gislason 1979; Pope 1979), it was necessary to introduce a proxy term to reconcile size-based feeding relationships with the age-based single-species assessment. Thus, in the MSVPA for the North Sea, the species- and age-based term suitability was introduced as an average North Sea wide valid index of diet selection. This term acts as a proxy for processes influencing the diet composition of a predator, i.e., prey species and size preferences as well as spatiotemporal overlap between predator and prey.

From both theory and field observations there are good reasons for suitabilities to vary with time, e.g., changes in size and structure of both predator and prey stock can lead to changes in distribution and therefore in spatiotemporal overlap as well as relative abundances of all prey types. Presently, suitability coefficients are assumed to be invariate with time, although analyses of the MSVPA suitability matrix revealed interannual variations (Rice et al. 1991; ICES 1994). Consequently, potential successors of the MSVPA model should have a more advanced dynamic diet selection submodel implemented, a possibility under discussion (ICES 1999). In a dynamic diet selection submodel, the individual processes underlying the diet selection behaviour need to be implemented separately. For example, in the boreal migration and consumption model (BORMICON; Stefánsson and Pálsson 1997), the functions for species and size preference as well as spatiotemporal predator–prey overlap can be

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parameterised individually. To be able to implement such a submodel in a North Sea multispecies assessment model, the preference functions and the relative significances of all underlying processes need to be known first.

In this analysis we determine and parameterise the size preference function of North Sea cod (*Gadus morhua* L.) feeding on fish and assess the relative significances that prey size preference and prey abundance have for the determination of the diet composition. The present analysis focuses on North Sea cod as a typical piscivorous predator. From earlier studies it is known that the diet of cod contains, even at small predator sizes, substantial fractions of fish (Bromley et al. 1997), which increase with increasing body length of the predator (Hislop et al. 1997). In the North Sea, cod is the only abundant predatory fish that grows large enough to feed on adult gadoids and, hence, to allow comparison over a wide length range.

The main difficulty in the evaluation of selective feeding at the individual level is to estimate the prey abundance in the ambient environment closest to the predator's true perception. The reconstruction of the actual feeding situation in the North Sea at a spatial and temporal scale small enough to be relevant for individual predators is not possible from the integrated information received from standard trawl surveys. Thus, instead of following an individually based approach, a size spectrum of potential fish prey in the North Sea was developed by aggregating available data over space and time. Correction methods were applied to address the effects of species- and size-specific catchability of the sampling gear. The species-specific catchability was addressed by applying the availability concept developed by Yang (1982) and Sparholt (1990). The size-specific catchability was addressed by calculating the size spectrum only from data of fish sizes that are caught quantitatively and then extrapolating the spectrum down to smaller fish sizes. The potential bias due to these corrections was addressed in a sensitivity analysis.

The target was to model the average prey fields at the North Sea level under consideration of prey availability at the intermediate scale, i.e., between the individual scale and the ecosystem level. To take the spatiotemporal overlap between cod and its prey into account, prey abundance was weighted during the calculation of the size spectrum by cod abundance in an area of 30 × 30 nautical miles (n.mi.).

The determination and parameterisation of the size preference function of North Sea cod feeding on fish was then conducted by calculating the selectivity coefficient (Vanderploeg and Scavia 1979). For the computation of the index, the relative prey abundances in certain size classes in the field were estimated from the modelled number spectrum and confronted with the respective fractions observed in the stomach contents of cod.

Materials and methods

Stomach content data

Information on the diet of cod was derived from the International North Sea Stomach Database (INSSB; Daan 1989; Hislop et al. 1997). Samples had been taken under the auspices of the International Council for the Exploration of the Sea (ICES). The quarter of the year is the temporal resolution of the data and the spatial resolution is the ICES statistical rectangle (30 × 30 n.mi.). Detailed descriptions of sampling and stomach content analysis procedures can be found in Robb (1991). Cod stomach content data used in this analysis stem from quarters 1 and 3 of the years 1980 to 1982, 1985 to 1987, and 1991 and from quarter 2 of the years 1980 to 1982, 1984, and 1991.

Only fish prey for which total length information had been provided was used for this study. Fish prey length was converted to weight by assuming isometric growth; predator weight was calculated from a length–weight relationship (Coull et al. 1989). Because of the limited amount of stomach content data in the extreme size classes, a year-specific analysis was not possible and data of all years were pooled by quarter. Over the years different predator and prey size classes were adopted during the surveys (Hislop et al. 1997). Thus, the data had to be recategorised to maximise the usable amount of information while keeping the size classes small. The resulting nine predator size classes (mm) are 100–149, 150–199, 200–249, 250–299, 300–399, 400–499, 500–699, 700–999, and 1000–1499. The seven prey size classes (mm) are 30–49, 50–99, 100–149, 150–199, 200–249, 250–299, and 300–399.

Predator–prey size-class combinations were only included in the analysis when at least five prey items had been observed. This study is based on the information gained from the analysis of 49 962 cod stomachs (Table 1).

Fish abundance data

To estimate the size-structured abundance of fish prey in the field, data from 12 years (1980–1991) of the 1st-quarter International North Sea Young Fish Survey (IYFS) and 5 years (1991–1995) of the 2nd- and 3rd-quarter International North Sea Bottom Trawl Survey (IBTS) were used. The well-standardised survey covered the whole North Sea area, and the Grande Ouverture Verticale (GOV) bottom trawl was the predominantly deployed gear (ICES 1992).

Combination of stomach and abundance data

Stomach samples of the 1st quarter were predominantly taken from the standard hauls of the IYFS. Therefore, most of the 1st-quarter stomach and abundance data used in this analysis were gathered in parallel from identical samples. Stomach and abundance data from the 2nd and 3rd quarter originate from different trawl hauls, because field abundance data from the 2nd and 3rd quarter of the period 1980–1990 were not available. The 2nd- and 3rd-quarter stomach content data stem from the period 1980–1991, but the corresponding estimation of fish prey in the sea was based on IBTS data from 1991–1995. The potential error resulting from this mismatch was addressed in the sensitivity analysis.

Estimation of fish prey in the sea by number spectra

Information of fish abundance taken from the IYFS and IBTS was used for the calculation of the number spectra. To take the spatial and temporal overlap between cod and its prey into consideration, the abundance of prey fish was weighted at the ICES statistical rectangle scale with the catch-per-unit-effort (CPUE) of cod.

To reduce the bias introduced by species-specific gear catchability, the field data on fish abundance were corrected

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Table 1. Number of cod stomachs analysed per size class and number of fish prey observed in the stomachs.

	Quarter 1		Quarter 2		Quarter 3	
Predator length classes (mm)	No. of stomachs with food	No. of observed fish prey organism	No. of stomachs with food	No. of observed fish prey organism	No. of stomachs with food	No. of observed fish prey organism
100–149	543	98	130	52	504	90
150–199	1 235	314	682	226	398	136
200–249	1 971	675	1 210	561	1 293	685
250–299	1 783	705	1 313	1 043	2 175	1 255
300–399	5 087	2 679	1 453	3 070	4 256	3 391
400–499	4 035	2 733	1 485	2 982	2 143	2 323
500–699	6 498	5 489	1 194	3 276	1 904	3 121
700–999	5 979	6 398	704	4 511	887	2 389
1000–1500	912	1 702	76	587	112	534
Total sum	28 043	20 793	8 247	16 308	13 672	13 924

Note: Numbers are sums over quarters of years 1980 to 1982, 1985 to 1987, and 1991.

using a modified version of a method developed by Yang (1982) and Sparholt (1990), who defined availability (A) as the ratio between the CPUE obtained from research vessel data and the true biomass of the stock in question. Estimates of true stock sizes were taken from the North Sea MSVPA results.

In our analysis the ratio of a species' CPUE in numbers and its corresponding MSVPA stock sizes for each year and quarter combination (A) was calculated. The stock numbers were taken from the 1997 key run of the North Sea MSVPA (ICES 1997), which provided numbers for 12 fish species. Hereafter, these species are referred to as MSVPA species. The MSVPA species were categorised into seven groups of roughly comparable habitat and behaviour. Average group- and quarter-specific availabilities were calculated as arithmetic means over the species-specific availabilities and all years. All other species that occurred in the survey and stomach content data but are not included in the MSVPA were allocated to one of the seven groups, according to similarities in behaviour and habitat.

The GOV-trawl 50% retention length (L_{50}) of Norway pout (*Trisopterus esmarkii* Nilsson) is approximately 8 cm with a narrow selection range of approximately 4 cm (Götz 1997). As there are no further species-specific L_{50} parameters known, catch data of all organisms below 15 cm were regarded as biased and not used for the estimation of fish prey in the sea. Hence, to be able to calculate the relative abundances of fish prey smaller that 15 cm in the field, a length-based number spectrum (Pope and Knights 1982; Rice and Gislason 1996) of the fish prey size distribution in the field was calculated for the unbiased size range and extrapolated downwards to smaller sizes.

For the construction of the North Sea wide number spectrum, the IYFS/IBTS standard haul was used consistently as the measure of fishing effort. The calculation procedure comprised the following steps.

The average catch rates in numbers per hour at the spatial scale of the ICES statistical rectangle ($C_{Y,Q,\mathrm{RA},\mathrm{SR},j,l}$) were calculated as the year- (Y) and quarter-specific (Q) mean catch rates in numbers per haul (H) for each species (j) and 1-cm length class (l) ($C_{Y,Q,H,j,l}$). The CPUE of cod ($C_{Y,Q,H,\mathrm{cod}}$) from the same hauls were used as a weighting factor to take the predator–prey overlap into account. The term $N_{Y,Q,\mathrm{SR}}$ denotes the number of hauls conducted per rectangle. This calculation was done for the size range from 15 to 80 cm (eq. 1).

$$(1)\qquad C_{Y,Q,\mathrm{RA},\mathrm{SR},j,l} = \frac{\sum_{H} C_{Y,Q,H,j,l} \cdot C_{Y,Q,H,\mathrm{cod}}}{N_{Y,Q,\mathrm{SR}}}$$

In a second step, these mean catch rates were averaged over ICES rectangles in each of the seven ICES roundfish areas (RA) to obtain the average catch rates at the spatial scale of the roundfish area ($C_{Y,Q,\mathrm{RA},j,l}$). As weighting factors, the number of fished rectangles in each RA ($\mathrm{NFSR}_{Y,Q,\mathrm{RA}}$) was used (eq. 2).

$$(2)\qquad C_{Y,Q,\mathrm{RA},j,l} = \frac{\sum_{\mathrm{SR}} (C_{Y,Q,\mathrm{RA},\mathrm{SR},j,l} \cdot \mathrm{NFSR}_{Y,Q,\mathrm{RA}})}{\sum_{\mathrm{RA}} \mathrm{NFSR}_{Y,Q,\mathrm{RA}}}$$

The mean catch rates for the total North Sea area (NS) were calculated by averaging the catch rates at the spatial scale of the roundfish area over all ICES RAs ($C_{Y,Q,\mathrm{NS},j,l}$), using the total number of rectangles per RA ($\mathrm{NSR}_{Y,Q,\mathrm{RA}}$) as weighting factors. All calculations were conducted per year, quarter, species, and 1-cm size class (eq. 3).

$$(3)\qquad C_{Y,Q,\mathrm{NS},j,l} = \frac{\sum_{\mathrm{RA}} (C_{Y,Q,\mathrm{RA},j,l} \cdot \mathrm{NSR}_{Y,Q,\mathrm{RA}})}{\sum_{\mathrm{RA}} \mathrm{NSR}_{Y,Q,\mathrm{RA}}}$$

Then, the $C_{Y,Q,\mathrm{NS},j,l}$ were corrected for their catchability by dividing them by their quarter- and group-specific availabilities (A). Subsequently, the catch rates were aggregated over species and 5-cm length classes and calculated as quarterly arithmetic means over the years. Eventually, three quarterly number spectra were calculated by a linear regression of the natural logarithm of weighted and corrected numbers caught versus the natural logarithm of the midpoints of the 5-cm length classes. With the derived parameters of the three quarterly regression lines, the length range was extrapolated downwards to fish sizes of 3 cm.

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From the three backtransformed number spectra, the quarterly relative size distributions of potential fish prey in the length range of 3 to 80 cm was derived and subsequently aggregated into the prey size classes. In addition to the three quarterly number spectra, a single average spectrum over all three quarters and all years was calculated. These four estimations of potential fish prey in the sea were subsequently used in the determination of the size preference function of North Sea cod feeding on fish.

To assess the effect of the interannual variability in the slopes of the quarterly number spectra on the size preference function, year- and quarter-specific number spectra were computed and the results were applied in the sensitivity analysis.

Index of preference

We used the selectivity coefficient W_i (eq. 4; Vanderploeg and Scavia 1979) as the mathematical measure of preference. This index is a normalised version of Shorygin's forage ratio (Ivlev 1961). It is normalised so that the sum of all ratios in a sample equals one. The selectivity coefficient W_i is identical to α_i as defined by Chesson (1978).

$$(4) \qquad W_i = \frac{r_i / p_i}{\sum_i^m r_i / p_i}$$

where r_i denotes the proportion of food type i in the predator's diet, p_i denotes the proportion of food type i in the environment, which is derived from the number spectra, and m is the number of prey types.

In comparison with nonnormalised indices, W_i has the advantage that its absolute value is independent of the relative abundance of the prey in the other size classes, which allows meaningful intersample comparisons. Because of its normalisation, the index can be thought of as representing the predators perception of the value of a food type i in relation to both its size and abundance and that of the other food types.

The index is bounded by the values 0 and 1, with values above $1/m$ indicating preference. When $W_i = 1/m$, prey type i is preyed upon randomly, values below $1/m$ indicate avoidance. This latter property makes the index rather unsuitable for presentation purposes. For graphical presentation, the index (E_i^*; eq. 5) of relative electivity (Vanderploeg and Scavia 1979) was used instead. It is based on W_i but takes the number of prey types into account. As a result, it has the convenient property of indicating random feeding with a zero value and a range from –1 to 1. In the present analysis, the use of either index (W_i, E_i^*) leads to the same prey size preference functions with identical optimum prey sizes. These peaks of the size preference functions were used for the calculation of the preferred predator-to-prey weight ratios.

$$(5) \qquad E_i^* = \frac{W_i - (1/m)}{W_i + (1/m)}$$

Preference function

For the development of the general prey size preference function, the stomach content data of all available years and quarters were pooled. Based on this data set, W_i was calculated for all predator and prey size classes and number spectrum slopes (a) in the range of $a = -15$ to -0.1.

To resolve the functional form of the effects of predator size and number spectrum slope on the log(preferred predator-to-prey size ratio), a regression analysis was conducted. For all slopes investigated, the effect of predator size was best described as a linear function ($p < 0.001$). The log(preferred predator-to-prey size ratio) was approximated best by a power function of the slope ($p < 0.001$) for all predator size classes. The two determined functional forms were then incorporated in the general prey size preference model (eq. 6), which was fitted to the logarithms of W_i using the Levenberg–Marquardt algorithm for nonlinear regression in SPSS™ 10.

$$(6) \qquad \ln(W_i) = a + b\left\{\ln\left(\frac{\mathrm{PW}}{p}\right) + k\mathrm{PS} + m\mathrm{Slope}^n\right\} + c\left\{\ln\left(\frac{\mathrm{PW}}{p}\right) + k\mathrm{PS} + m\mathrm{Slope}^n\right\}^2$$

where PW denotes the predator weight (in g), PS denotes the predator size (in mm), p denotes the prey weight (in g), "Slope" is the absolute value of the slope of the number spectrum, and a, b, c, k, m, and n are constants. The preferred prey weight (PPW) for a certain predator weight and a specific slope of the number spectrum is represented as the maximum of eq. 6 and can therefore be estimated from its first derivative (eq. 7):

$$(7) \qquad \mathrm{PPW} = e^{\left(\frac{b}{2c} + k\mathrm{PS} + m\mathrm{Slope}^n\right)}\mathrm{PW}$$

From that it follows that the preferred predator-to-prey weight ratio (PWR) for a certain predator weight and a specific slope of the number spectrum then becomes (eq. 8)

$$(8) \qquad \mathrm{PWR} = e^{\left(\frac{b}{2c} + k\mathrm{PS} + m\mathrm{Slope}^n\right)}$$

Sensitivity analysis

Two aspects of the methods applied here might have been major sources of bias: (*i*) the use of average quarterly number spectra instead of year-specific quarterly spectra and (*ii*) the linear extrapolation of the number spectra down to smaller sizes.

To investigate the bias in the resulting preferences resulting from the averaged quarterly size spectra, the preference indices were recalculated using extreme values observed. Two extreme number spectra of each quarter were applied, which represent the steepest and the flattest slopes observed during the respective periods. In this approach two sets of size preference indices were calculated from the quarterly pooled stomach content data in combination with the extreme year- and quarter-specific number spectra.

Although the number spectrum in the range of 15 to 80 cm was based on data, the lower size range was linearly extrapolated. To test the influence of the extrapolation, the slope of the extrapolated part of the 1st-quarter number spectrum (a) was varied systematically from 0 to –10 and combined with the constant average 1st-quarter slope in the

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size range above 15 cm. The resulting discontinuous number spectrum was used for the recalculation of the size preference indices.

Significance of prey size preference

To quantify the significance of prey size preference for the determination of the diet composition cumulated fractions of prey over increasing size classes observed in the stomachs were plotted versus their cumulated preferences. For this analysis, the index W_i (eq. 4) was used, because it conveniently ranges from 0 to 1.

Results

Potential fish prey in the sea

The hierarchy of the average availabilities (A) for the 12 MSVPA species in the period from 1980 to 1991 matches common knowledge on species ecology (Table 2). The 1st-quarter average A of sandeels in the GOV trawl was almost 17 000 times lower than that of haddock, the species with the highest A. As the result of averaging over species within groups, the difference in the availabilities between the highest (1) and the lowest (7) availability group was reduced to a factor of approximately 9000. On the other hand, the intragroup variation between the single-species availabilities was comparatively low, a factor of 7.4 in group 1 at maximum.

The parameters of the quarterly number spectra of potential prey in the North Sea for different years vary substantially (Table 3). In the 1st quarter of 1983, the intercept was highest and slope was steepest, i.e., a comparatively high amount, in relative as well as in absolute terms, of small-sized fish had been available as prey. The opposite was true in 1985. To demonstrate the effects of taking the species-specific gear catchability into account, the slopes of the uncorrected size spectra are provided in parallel. In 11 of 12 years, the uncorrected 1st-quarter slopes were flatter (about 2–28%) than the corrected version. In quarters 2 and 3, all uncorrected slopes were flatter (quarter 2 about 5–22%; quarter 3 about 11–31%) than the corrected size spectra. The application of the uncorrected spectra generally resulted in even higher PWR than obtained by the corrected size spectra.

Prey size preference

The relative preference of cod of different sizes for fish prey of different sizes, expressed as the index of relative electivity (E_i^*) showed that the smallest prey size classes were always avoided (Fig. 1). The preferred prey size class increased with an increase in predator length. For intermediate-sized predators the plot is an optimum function, the curve for the smallest and the largest predators is restricted to the increasing left limb. With increasing predator size the top of the optimum curve broadens, i.e., the preference differences between neighbouring prey size classes become smaller.

PWR is an increasing function of predator size, i.e., as predators grow, they prefer on average relatively smaller prey (Fig. 2). The increase is most pronounced in cod larger than 40 cm. This applies to quarters 1 to 3 separately, as well as for all quarters combined. In quarter 2 the PWR for cod larger than 30 cm tended to be higher than in the other quarters.

The general prey size preference function (eq. 6) explained 97% of the variance with 719 degrees of freedom (Table 4). The modelled prey size preference resulted in an exponentially increasing PWR as a function of predator size (eq. 8; Fig. 2). For quarter 2 there was a tendency for the PWRs predicted from the model to be lower than the PWRs calculated directly from the data, whereas for quarter 3, the opposite was true.

The first part of the sensitivity analysis revealed that the largest impact of an extreme annual slope of the size spectra on the PWR was observed in quarter 1 (Fig. 3*a*). The application of the steepest slope (year 1983) resulted in a deviation of the PWR of cod size class 50–69 cm by a factor of 0.55 compared with the results of the average quarter-1 model for the period 1980 to 1991 (Fig. 3). The use of the flattest slope (year 1985) resulted in deviations between the PWRs in the range of zero (for cod 20–29 cm) to a factor of 8 for the largest size class compared with the results of the average model. In quarters 2 and 3 the deviations were below a factor of 2.7 and 2.1, respectively (Figs. 3*b*, 3*c*). The general pattern was that flatter slopes lead to higher PWRs, as expected. However, steeper slopes tend to give the same results as the mean slopes. The overall increasing PWR with increasing predator size was robust in any case. Systematically changing the slope of the number spectrum in eq. 8 demonstrated that the derived PWRs increased exponentially with predator size, whereas the PWR of a certain predator size class decreased exponentially with increasing steepness of the slope (Fig. 3*d*).

The second part of the sensitivity analysis showed that systematically changing the slope of the extrapolated part of the number spectrum revealed significant impacts on the PWRs of smaller cod (Fig. 4). Overall, the application of extrapolated slopes steeper than the average slope maintained the increasing trend in the PWR as a function of predator size. Extrapolated slopes flatter than the average spectrum resulted in a more complex picture, but in all cases, the preferred weight ratio increases with an increase in predator size for cod larger than 50 cm. For smaller cod, slopes in the range of $a = -4$ to -3 resulted in a decrease of the PWR with increasing predator sizes. At even flatter slopes ($a = -2$ to 0), a peak of PWRs at a predator length of 25–30 cm occurred.

The quantification of the significance of prey size preference for the determination of the diet composition of cod demonstrated that prey abundance is the main forcing factor. The graphical analysis clearly revealed that in all three quarters and in the complete predator size range, more than 75% of fish found in the stomachs stem from the least preferred quarter of the potential fish prey in the sea (Fig. 5).

Discussion

Prey size preference

The analysis of prey size preference shows that for cod feeding on fish the PWR is an increasing function of predator size, i.e., the fraction of relatively small fish in the diet composition of North Sea cod progressively increases with

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Table 2. Quarterly availability (A) terms for multispecies virtual population analysis (MSVPA) species and average availabilities of the seven species groups.

MSVPA species	Species availability, h^{-1}			Group No.	Group availability, h^{-1}		
	Quarter 1	Quarter 2	Quarter 3		Quarter 1	Quarter 2	Quarter 3
Melanogrammus aeglefinus	9.79×10^{-4}	1.17×10^{-3}	2.43×10^{-4}	1	5.34×10^{-4}	8.00×10^{-4}	1.60×10^{-4}
Merlangius merlangus	8.25×10^{-4}	1.52×10^{-3}	2.17×10^{-4}	1	5.34×10^{-4}	8.00×10^{-4}	1.60×10^{-4}
Gadus morhua	2.02×10^{-4}	3.41×10^{-4}	4.73×10^{-5}	1	5.34×10^{-4}	8.00×10^{-4}	1.60×10^{-4}
Eutrigla gurnardus	1.32×10^{-4}	1.77×10^{-4}	1.37×10^{-4}	1	5.34×10^{-4}	8.00×10^{-4}	1.60×10^{-4}
Clupea harengus	2.94×10^{-4}	9.93×10^{-4}	3.64×10^{-4}	2	2.94×10^{-4}	9.93×10^{-4}	3.64×10^{-4}
Pollachius virens	7.03×10^{-5}	6.01×10^{-5}	5.85×10^{-5}	3	5.86×10^{-5}	9.90×10^{-4}	3.60×10^{-4}
Trisopterus esmarkii	4.70×10^{-5}	1.08×10^{-4}	1.84×10^{-5}	3	5.86×10^{-5}	9.90×10^{-4}	3.60×10^{-4}
Pleuronectes platessa	3.00×10^{-5}	3.60×10^{-5}	3.87×10^{-5}	4	2.52×10^{-5}	3.50×10^{-6}	5.10×10^{-8}
Raja radiata	2.05×10^{-5}	1.58×10^{-5}	2.46×10^{-5}	4	2.52×10^{-5}	3.50×10^{-6}	5.10×10^{-8}
Scomber scombrus	1.83×10^{-5}	1.46×10^{-4}	9.21×10^{-5}	5	1.83×10^{-5}	1.46×10^{-4}	9.21×10^{-5}
Solea solea	8.39×10^{-7}	6.04×10^{-7}	2.49×10^{-6}	6	8.39×10^{-7}	6.04×10^{-7}	2.49×10^{-6}
Ammodytes spp.	5.83×10^{-8}	5.11×10^{-8}	3.28×10^{-7}	7	5.83×10^{-8}	5.11×10^{-8}	3.28×10^{-7}

Table 3. Quarter-of-year and average slopes in the period 1980 to 1995 of the A-corrected and uncorrected prey number spectra for quarters 1 to 3.

Year	Quarter 1		Quarter 2		Quarter 3	
	Corrected	Uncorrected	Corrected	Uncorrected	Corrected	Uncorrected
1980	–6.69	–5.33				
1981	–7.49	–6.05				
1982	–6.63	–5.88				
1983	–7.60 (max.)	–5.42				
1984	–6.62	–6.13				
1985	–3.54 (min.)	–3.29 (min.)				
1986	–7.47	–6.37				
1987	–7.11	–6.90 (max.)				
1988	–6.3	–5.6				
1989	–7.15	–6.06				
1990	–6.94	–6.23				
1991	–6.3	–6.45	–8.24	–6.53	–8.09	–7.19
1992			–8.34	–6.66	–10.43 (max.)	–7.23
1993			–6.38 (min.)	–6.06 (min.)	–9.55	–7.16
1994			–8.79 (max.)	–6.87 (max.)	–9.87	–7.74 (max.)
1995			–7.78	–6.49	–8.03 (min.)	–6.18 (min.)
Mean	–6.37	–5.37	–8.03	–6.51	–9.92	–7.33

Note: Linear regressions were performed in the range of 15–80 cm. All regressions are significant at $p < 0.001$. Mean, minimum (min.), and maximum (max.) slopes used in the sensitivity analyses are indicated.

predator size. More than 75% of fish found in the stomachs of North Sea cod originated from the least preferred quartile of the size range.

From IBTS observations it is known that the slopes and intercepts of the number spectra of the North Sea fish assemblage have become steeper, respectively higher, over the period from 1973 to 1993 (ICES 1996), a result that remains valid for the A-corrected number spectra (Floeter 1998). A modelling study has demonstrated that the slope and the intercept of the size spectrum of 11 North Sea MSVPA species vary proportional to changes in fishing intensity (Gislason and Rice 1998). Hence, when prey size preference is regarded as an evolutionarily determined aspect of behaviour, the result that North Sea cod feeds predominantly on least-preferred prey sizes may indicate a too-slow behavioural adaptation to a rapidly changing environment under intense human harvest. On the other hand, the fact that North Sea cod is able to successfully live on a diet more than 75% of which consists of least-preferred prey sizes may indicate that it is a highly adaptable species, which is evolutionarily well prepared to survive in rapidly changing environments.

Methodology

As a result of using discrete size classes, a methodological artefact occurred in some cases. Despite an inherent trend in size preference with increasing predator size, some predators of neighbouring size classes apparently preferred equal-sized prey. This was caused by the use of prey size classes that were too wide. The achievable resolution of prey sizes in the analysis was evidently coarser than the biologically signifi-

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Fig. 1. Size preference of cod (*Gadus morhua* L.) for fish prey of different sizes, depicted as index of relative electivity E_i^*. A value of $E_i^* = 0$ stands for random feeding, positive values indicating positive preference, negative values indicating avoidance. Results of the mean *A*-corrected prey number spectrum over quarters 1–3 are presented.

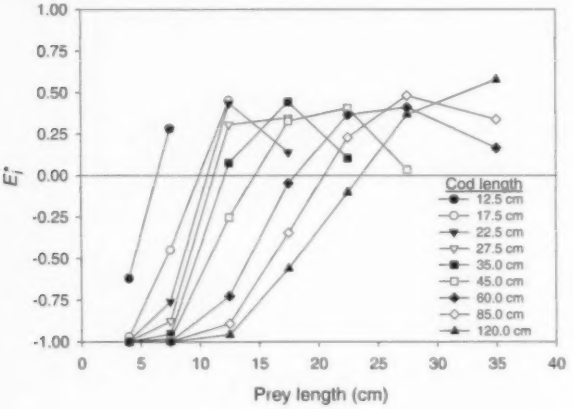
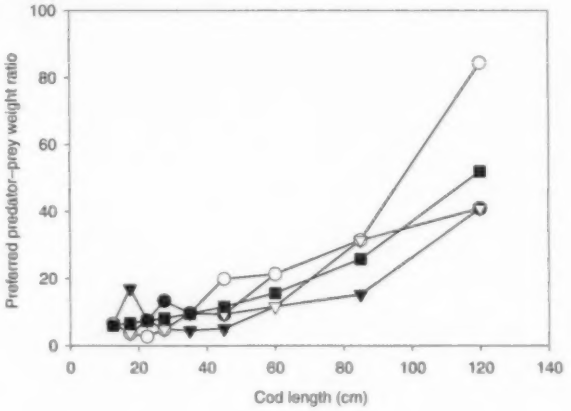


Fig. 2. Preferred predator-to-prey weight ratios as a function of cod (*Gadus morhua* L.) size. Results of the mean *A*-corrected prey number spectrum for quarters 1, 2, and 3 and the average *A*-corrected spectrum over quarters 1–3 are presented: ●, quarter 1; ○, quarter 2; ▼, quarter 3; ▽, average of quarters 1 to 3; ■, prey size preference model.



cant differentiation of prey sizes exerted by the cod. This artefact had only a marginal effect on the general prey size preference model because it took into account all predator and prey size classes simultaneously.

The sensitivity analysis performed demonstrated that the results are robust with regard to possible over- or underestimation of available prey in the field. The effect of the quarterly availabilities, as well as the application of quarterly minimum and maximum slopes, showed that the increasing trend in the PWR is likely to be even more pronounced than reversed. In contrast, a pronounced overestimation of small prey in the field would significantly affect the shape of the PWRs in smaller cod, reversing the trend and leading to a more U-shaped PWR. However, the probability of substantially overestimating the fraction of small fish in the field can be regarded as low, because the analysis covers the quarters of the year when production is highest. Even if the slope of the extrapolated part of the spectrum is set to zero, only the smallest cod size class would appear to feed predominantly on prey that stem from the preferred half of the size range. For all other size classes, the result that more than 75% of fish found in the stomachs originated from the least-preferred quartile of the size range remained true.

Comparison with former analyses of prey size preference

The result that the PWR is an increasing function of predator size is in disagreement with former results from weight-based analyses that use Ursin's size-preference function for cod and dab (*Limanda limanda* L.) feeding on benthic invertebrates (Ursin 1973; Andersen and Ursin 1977) and its extension by Andersen (1981). Ursin (1973), assuming a Sheldon-type flat biomass spectrum with zero slope, described the prey size preference of predators as a lognormal frequency distribution of predator-to-prey weight ratios, i.e., predators have a constant ratio based trophic niche breadth and prey size preference is independent of predator size. The peak of the distribution marks the PWR and was referred to as the constant η. Thus, the preferred absolute prey weight increases proportionally to the absolute predator weight. Dekker (1983), applying a subset of the 1981 INSSB data to Ursin's methodology, calculated a PWR of $\eta = 66$ for North Sea cod feeding on fish. Horbowy (1982) determined prey species specific PWRs of $\eta = 135$, 120, and 55 for Baltic Sea cod preying on sprat, herring, and young cod, respectively. In general, the PWRs calculated by Ursin's (1973) weight-based function are consistently higher than the PWRs derived from our size-based approach, which may be an effect of both (*i*) the problems inherent in weight measurements of partially digested prey and (*ii*) the a priori prohibition of changes in PWR with predator size in Ursin's equation.

Bundgaard and Sparholt (1992) performed a length-based analysis of prey size preference in Baltic Sea cod preying on herring (*Clupea harengus* L.) and sprat (*Sprattus sprattus* L.). According to their findings, the PWR was not constant but rather increased as a function of predator size, thus agreeing with our results. Their prey species specific PWR of equal-sized cod for sprat was higher than that for herring (PWRs ranging from 28 to 190 for herring and 42 to 408 for sprat) and higher than in our analysis. This probably reflects their calculation of species-specific preferences which limits the available prey size range. As in absolute terms larger predators generally prey on larger prey, the situation can arise that predators already feed on the largest individuals of a prey species. Subsequently, the η for this prey species increases, although the predators would prefer even larger prey. Thus, this η does not reflect the predators PWR anymore and can be referred to as an apparent prey size preference that mirrors specific ecosystem properties of cod feeding in the Baltic Sea rather than inherent prey size preference of cod.

The question arises as to in which cases an aggregated view on the prey species in a predators diet inevitably leads to an increasing function of PWR with increasing predator size. This would be true if the average diet compositions of

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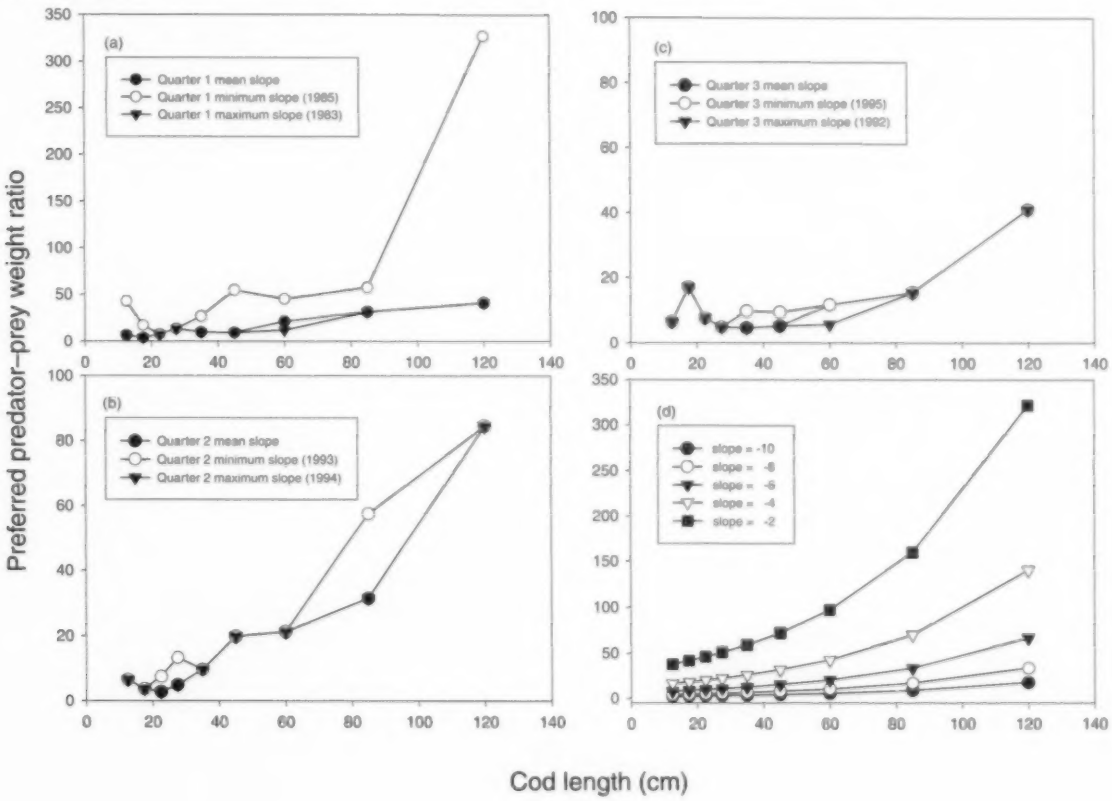
Table 4. Parameters of the general prey size preference model (eq. 6) fitted to the logarithms of the selectivity coefficients (W_i) using the Levenberg–Marquardt nonlinear regression algorithm in SPSS™ 10.

	Degrees of freedom	Sum of squares	Estimate	Standard error	95% confidence interval	
					Lower	Upper
Regression	12	40 637.85				
Residual	708	640.41				
Corrected total	719	24 799.83				
R^2	0.97					
Parameter						
a			–9.412	0.071	–9.551	–9.273
b			3.921	0.023	3.876	3.966
c			–0.436	0.28	–0.986	0.114
k			–0.002	0.006	–0.015	0.01
m			0.647	0.049	0.551	0.744
n			0.797	0	0.797	0.797

Fig. 3. Sensitivity analysis. The impact of the slope of the number spectrum on the preferred predator-to-prey weight ratio as a function of predator length. Results from application of the mean, maximum, and minimum slopes from the period 1980 to 1991 (*a*, quarter 1) and the respective slopes from the period 1991 to 1995 (*b*, quarter 2; *c*, quarter 3) are presented. Stomach data stem from respective quarters. (*d*) The results from application of systematically varying slopes to the general prey size preference model (eqs. 6 and 8) are presented.



increasingly larger predators systematically shift towards a progressively higher fraction of prey species with a smaller maximum size. However, this is not the case in North Sea cod (Hislop et al. 1997; Floeter 1998).

Analysis of the hypothesis of a constant PWR

Former analyses were based on the assumption of a constant particle (prey) biomass distribution within equal logarithmic intervals of particle diameter (Ursin 1973; Horbowy

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Fig. 4. Sensitivity analysis. The impact of the extrapolated slope of the number spectrum under 15 cm on the preferred predator-to-prey weight ratio as a function of predator length.

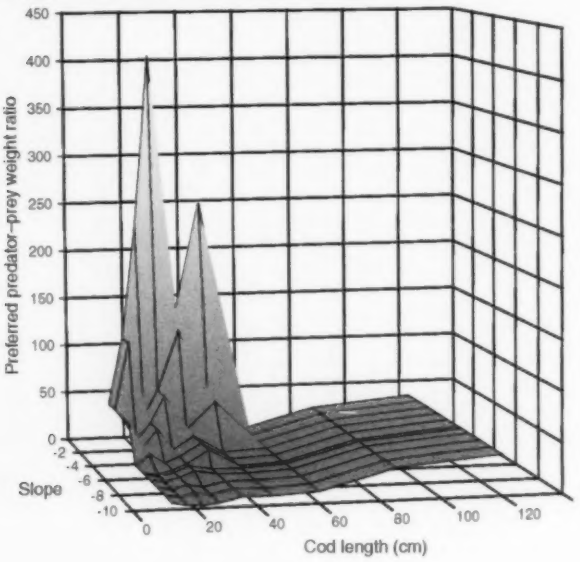
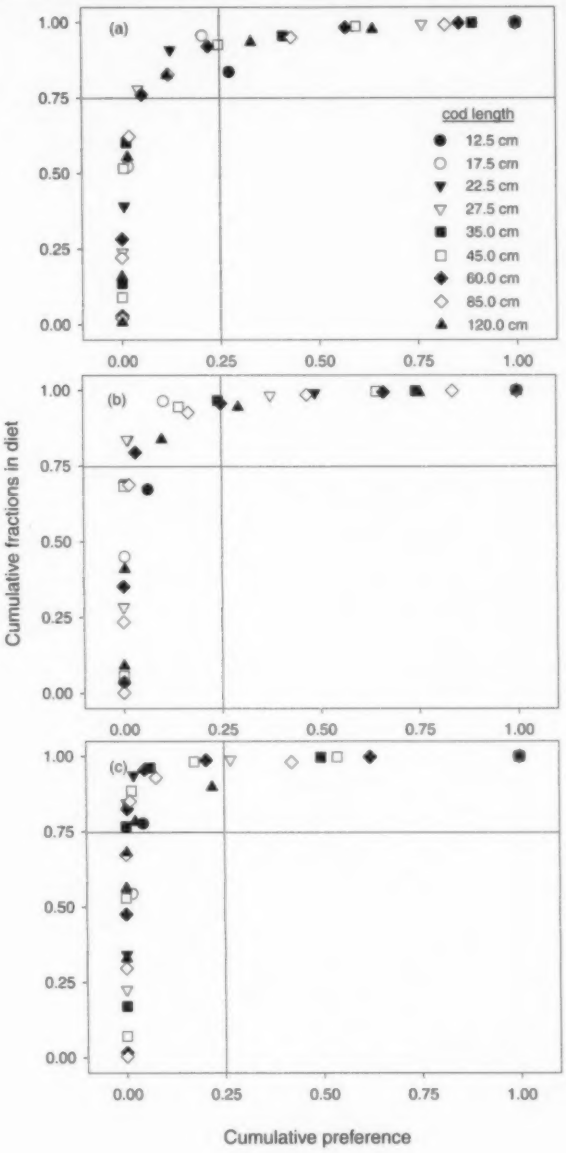


Fig. 5. Cumulative fractions of fish prey in the stomach versus cumulative size preference. Results from application of the mean quarterly slopes (*a*–*c*, quarters 1–3, respectively) are presented.



1982; Dekker 1983), i.e., a flat biomass spectrum with zero slope (Sheldon et al. 1972). While it is widely accepted that the slope of the overall or primary biomass spectrum is zero or slightly negative over larger areas and in an annual average, this is not true at the seasonal scale (Kerr and Dickie 2001). Moreover, the secondary scaling of the biomass spectrum consists of a series of domes with steeper slopes, each dome representing discrete trophic positions, e.g., fish, that have common production efficiencies (Boudreau and Dickie 1992). For a comparison with the earlier analyses, we transformed the length-based number spectra used in our analysis into the corresponding biomass spectra. The slopes of these biomass spectra were all negative, varying from –1.8 to –2.1. Hence, the assumption of a constant prey biomass spectrum with zero slope is not valid with respect to the fish assemblage in the North Sea.

Following the hypotheses of a constant prey biomass spectrum with zero slope, Ursin (1973) concluded that the potential food resource is independent of predator size because the ratio-based trophic niche breadth is constant. Subsequently, Ursin concluded that the PWR has to be independent of predator size. That the niche breadth on a log scale is constant as the predator grows was generally confirmed by a statistical reanalysis of published data on predator and prey size relationships (Pearre 1986). However, Pearre (1986) also demonstrated mathematically that the negative slope of the biomass spectrum implies a decreasing potential prey biomass for a growing predator with increasing mean prey size in the diet. The magnitude of this effect depends on the slope of the biomass spectrum. Thus, it can be stated that the potential fish food resource for North Sea cod decreases substantially as it grows, because the fish biomass spectra has a negative slope. This means that although the ratio-based trophic niche breadth is generally constant, the PWR is not independent of predator size because the slope of the prey spectrum is not zero.

Moreover, the decline in potential fish prey resource is probably more severe than indicated by the slope of the spectrum of standing biomass, because predators utilize production not biomass (Kerr 1974). And as productivity generally declines with size (e.g., Fenchel 1974), the food resource ($(P/B)B$) within any constant or decreasing biomass interval must decrease as the mean prey size increases. This agrees well with an analysis of Baltic Sea whiting preying on fish: Ursin and Arntz (1985) differentiated two feeding

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modes, preferential and size-indiscriminate feeding of large numbers of invertebrate prey much smaller than actually preferred. The latter feeding mode was hypothesised to occur in predators under food scarcity, as may be the case for middle-sized whiting in the Baltic Sea or for large cod in the North Sea (Daan 1973). Following Ursin and Arntz (1985), the increase of PWR in large predators observed in our study may be a result of nonselective feeding rather than a change in size preference with predator size.

The fraction of invertebrates in the diet of North Sea cod decreases with increasing body size (Hislop et al. 1997). The effect of not including invertebrate prey in this analysis of prey size preference can only be discussed hypothetically, because there is no information on the number spectrum of invertebrates in the North Sea available. Depending on the slope of the invertebrate size spectrum, including the invertebrate prey fraction in the analysis may lead to either an increase or decrease in the PWR of smaller predators, while leaving the PWR of larger cod almost unaffected in any case.

Implications for recent concepts in multispecies fisheries modelling

In temperate seas, commercial fisheries are often mixed, fishing several species. This has led to the idea of developing aggregated multispecies assessment models based on interactions between groups of species instead of single species. Compared with species-specific multispecies assessment models, such aggregated models could have the ability to provide more robust results on the effects of certain management decisions on the multiannual time scale, which in addition are directly linkable to mixed fisheries. One type of such aggregated models, which should be used in a model suit together with species-specific models, is the size-spectrum model applied to fisheries management (e.g., Duplisea and Bravington 1999). Because of the strong functional link between the general prey size preference model and the slope of a number spectrum, our preference model is well suited for a direct implementation in a size-spectrum fisheries model.

The results of this study showed that prey size avoidance is by far more pronounced than positive preference, indicated by the steeply increasing left limb and the rather broad peaks of the preference function. Despite the sharp increase in preference at small prey sizes, more than 75% of fish found in the stomachs of North Sea cod originated from the least-preferred quartile of the size range. This means that prey abundance rather than prey size preference is by far the dominant force determining the size composition of the fish diet of North Sea cod. Thoroughly tested submodels on predator functional response and diet selection in marine temperate fish are not available yet (Floeter and Temming 2001). With respect to present concepts in multispecies fisheries modelling, our results can provide guiding ideas for future efforts. First, our analysis demonstrated that predator size effects on prey size preference have to be addressed in future diet-selection models. However, one should not overestimate the role of diet-selection models in overcoming the questionable assumption of constant age-based suitabilities in multispecies recruitment prediction models, because, second, the functional understanding of the dynamics in spatiotemporal predator–prey abundance and overlap seems to be the key task.

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pH 6 as the threshold to use in critical load modeling for zooplankton community change with acidification in lakes of south-central Ontario: accounting for morphometry and geography

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Abstract: Identifying thresholds of biotic community change along stressor gradients may be useful to both ecologists and lake managers; however, there are several weaknesses in the thresholds that have been identified for zooplankton communities along acidity gradients. The thresholds are often based on a single species even though pH sensitivities vary among species. They often measure changes in species occurrences, though abundances may be a more responsive indicator of damage. Their identification may be confounded by spatial and morphometric factors if they are derived from lake surveys. Finally, the thresholds have usually been subjectively identified. Our goal was to establish a threshold in zooplankton community change along an acidity gradient that did not have these four common weaknesses. We used two crustacean zooplankton community metrics: species richness and scores of a correspondence analysis based on species abundances. Spatial and morphometric patterns were detected in the zooplankton community data and then extracted. The relationship between zooplankton and acidity was then modeled using a step function that objectively identified a threshold of community change at pH 6 for lakes in south-central Ontario.

Résumé : L'identification des seuils des changements dans les communautés biotiques le long de gradients de stress peut être utile aux écologistes et aux gestionnaires de lacs; il y a, cependant, plusieurs faiblesses dans les seuils identifiés jusqu'à maintenant pour les communautés de zooplancton le long de gradients d'acidité. Les seuils sont souvent basés sur une seule espèce, même si la sensibilité au pH varie d'une espèce à une autre. Ils mesurent généralement des changements dans la fréquence des espèces, alors que les abondances sont peut-être des indicateurs plus efficaces de la présence de dommages. Leur identification peut être faussée par des facteurs spatiaux ou morphométriques lorsqu'ils sont basés sur des inventaires de lacs. Enfin, les seuils sont couramment identifiés de façon subjective. Notre but était d'établir un seuil qui ne souffre pas de ces quatre faiblesses habituelles pour le changement dans les communautés de zooplancton le long d'un gradient d'acidité. Nous avons utilisé deux métriques des communautés zooplanctoniques — la richesse en espèces et les positions dans une analyse des correspondances basée sur l'abondance des espèces. Des structures spatiales et morphométriques ont été décelées dans les données sur les communautés zooplanctoniques et elles ont été retirées. La relation entre le zooplancton et l'acidité a ensuite été modélisée à l'aide d'une fonction pas à pas qui a identifié de façon objective un seuil de changement de communauté à pH 6 dans les lacs du centre-sud de l'Ontario.

[Traduit par la Rédaction]

Introduction

The effects of acid rain have been severe. As a large number of species are acid sensitive, there have been decreases in species richness in various groups of aquatic biota (Minns et al. 1990; Matusek et al. 1992). In an effort to stop further damage and allow biotic recovery, legislation was introduced in the 1980s to regulate SO_2 emissions in eastern Canada and the U.S.A. These reductions have resulted in a 30–40% decrease in S deposition compared with 1980 levels and some increases in lake alkalinity and pH (Stoddard et al. 1999). To evaluate the success of these emission reductions, we should begin by comparing recent pH levels with the thresholds that distinguish damaged from undamaged lakes. However, despite years of research, it is still unclear at what pH biological damage unequivocally occurs.

The central difficulty in identifying this threshold is that it is a management issue with both scientific and nonscientific, or value-based, components. Acid sensitivity varies among species, whereas species composition varies among regions; thus, any threshold selected will likely vary among regions. This is the factual, science-based component of threshold selection. The degree of protection desired is the value-based component. Although this component is, to a degree, arbitrary and unpredictable, it is important that it be overtly ac-

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knowledged and, once acknowledged, the method of identifying the threshold be as objective as possible.

Existing thresholds of zooplankton community change have been identified along gradients in pH in space and time (Locke and Sprules 1993; Jeffries 1997). However, the identification of these thresholds may have been compromised by four factors. (1) Thresholds based on one or a few species, e.g., brown trout (*Salmo trutta*), might not protect the whole biotic community, as acid sensitivity varies enormously among taxa (e.g., Havens et al. 1993). (2) Thresholds based on species occurrences may underestimate damage attributable to changes in the relative abundances of taxa (e.g., Keller et al. 1990). (3) Thresholds developed from compositional patterns in synoptic surveys rarely extract unique acid signals. Instead, zooplankton metrics are usually also influenced by lake morphometry (Yan et al. 1996) or geography (Pinel-Alloul et al. 1995). (4) Finally, thresholds are rarely identified objectively (e.g., Keller and Pitbaldo 1984). In summary, we have yet to use an objective method to identify zooplankton community thresholds of change along acidity gradients that are not confounded by morphometry or geographic location and that reflect a clearly stated degree of desired protection.

The purpose of this study is to correct this situation, i.e., to identify a threshold of change in zooplankton community structure in south-central Ontario lakes along a pH gradient accounting for variability attributable to spatial and morphometric factors. Specifically, our objectives are (1) to determine if zooplankton community composition varies with lake location and morphometry in a data set previously shown to exhibit compositional change with pH, (2) to remove the variability associated with spatial and morphometric factors, if it exists, (3) to fit a model to the changes in the zooplankton community (corrected for spatial and morphometric factors) along a gradient in pH from which a threshold can be identified, (4) to objectively identify this threshold, and finally (5) to indicate what degree of protection this threshold should provide in the particular region, i.e., to acknowledge the value component of the threshold selection process.

Materials and methods

Study sites

We analyzed existing zooplankton and water chemistry data from 47 lakes (Yan et al. 1996) in the County of Haliburton and Districts of Muskoka, Parry Sound, and Nipissing (Ontario, Canada). The study lakes were typical of eastern temperate Canadian Shield lakes, and none has been subject to any experimental manipulations. They ranged in area from 7.2 to 679 ha (mean 95.5 ha). They had low concentrations of dissolved organic carbon (DOC) (mean 3.31 $mg \cdot L^{-1}$), Ca (mean 113.3 $\mu equiv. \cdot L^{-1}$), and total phosphorus (TP) (mean 7.9 $\mu g \cdot L^{-1}$). The pH and alkalinity of the lakes ranged widely (5.3–6.7 and –0.1–6.2 $mg \cdot L^{-1}$ as $CaCO_3$, respectively, at the time of sampling), mainly because of differences in the buffering capacity of their catchments (Neary and Dillon 1988). In heavily stained lakes, organic acids can be a major source of acidity. In our study lakes, the range of DOC was small, i.e., 10th to 90th percentile range of 1.8–5 $mg \cdot L^{-1}$. Equivalent ratios of sulphate to organic anion concentrations, calculated following Oliver et al. (1983), indicated that the dominant source of acidity in all of the study lakes was atmospheric deposition of strong acids. The descriptive statistics of this ratio for the 47 lakes were minimum (2), 25th percentile (5.1), median (9.1), 75th percentile (13), and maximum (415).

Zooplankton were sampled in the lakes at least monthly during the ice-free season for 1 year (1983, 1984, 1987, or 1988). Zooplankton species richness was predictable from, and increased with, increases in pH as well as in lake area ($r^2 = 0.60$; Yan et al. 1996). This data set is unique for several reasons. The lakes were chosen to have a uniform frequency distribution with pH over the entire pH gradient (pH 5.3–6.7) typical of the south-central Canadian Shield. Nine additional study lakes, including several humic lakes, that were chemical or morphometric outliers were removed (Yan et al. 1996). Consistent methods were used, i.e., the same collection gear was deployed in lakes in the same manner under the direction of the same field technician, and the crustacean zooplankton were subsequently counted by the same person using the same protocol under the direction of the same scientist (N.D. Yan).

Community metrics

Two metrics were used to compare zooplankton communities among the lakes: crustacean species richness and ordination scores from a multivariate analysis based on species abundances. Species richness was chosen because it has a consistent monotonic relationship with pH in synoptic zooplankton surveys across eastern North America (Sprules 1975*b*; Locke et al. 1994; Yan et al. 1996). This metric is considered an excellent acid indicator (Marmorek and Korman 1993) despite the well-known dependence of species richness on the number of individuals counted, sampling regime, and calculation method (Fisher et al. 1943). We calculated species richness as the ice-free season average of the number of species detected in standard counts of a minimum of 250 individuals in monthly collections. Multivariate metrics have the potential of being more sensitive to acidity than richness because they reflect changes in both the relative abundances of species and their covariations (Yan et al. 1996). Species abundances were compared among lakes using correspondence analysis (CA) scores of the species counts (in Statistica v.5.1; ter Braak and Verdonschot 1995). CA was used because it is not limited to linear patterns in species abundances; it is more robust to data standardizations than other multivariate techniques (Jackson 1993); and CA species ordination scores have shown patterns with acidity in previous studies (Siegfried and Sutherland 1992; Locke et al. 1994; Yan et al. 1996). The species count data were log transformed prior to analysis to downweight dominant species. A small constant was also added to each logged abundance ($\log(x + 1) + 0.2$) (Rusak et al. 2001) to further downweight species that were common in just a few lakes. Rare species (those which were encountered <10 times or in <5 lakes) were excluded. Immature cladocerans were identified and counted, but immature copepods were excluded.

Statistical methods

Objective 1

Spatial patterns in the zooplankton community data were

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identified by comparing geographic distances between lake pairs with zooplankton distance matrices using Mantel tests (in NTSYS v.2.01d; Legendre 1993). Two zooplankton distance matrices were constructed. The species richness distance matrix was constructed from the absolute differences in species richness between all pairs of lakes. Species abundance matrices were constructed using Euclidean distances of CA scores.

Patterns in zooplankton community structure linked with lake morphometry have previously been detected in this data set (Yan et al. 1996). The specific geographic and morphometric factors affecting zooplankton were identified using multiple regression for species richness and canonical correspondence analysis (CCA) for species abundances (ter Braak and Verdonschot 1995). Forward selection procedures were used, and the spatial variables considered were latitude, longitude, their interaction (latitude × longitude), and their polynomials (quadratics and cubics). The interaction and polynomial terms were included so as not to limit the search to linear spatial patterns. The morphometric variables considered included lake area, log of lake volume, maximum depth, and mean depth.

Objective 2

The variance in community structure related to spatial and morphometric factors was removed from the total variance through partial multiple regression in the univariate case (species richness) and CA with spatial and morphometric variables as covariables in the multivariate case (species abundances) (Legendre and Legendre 1998). In this way, patterns in zooplankton communities that could be uniquely ascribed to acidity were identified.

Objective 3

Changes with pH in the "unique" (i.e., unconfounded by spatial and morphometric factors) zooplankton community metrics were modeled using both linear and step functions. The linear model was calculated using a least squares method. The step function model was calculated using regression tree analysis (Brieman et al. 1984). This analysis uses recurrent binary partitioning to calculate that split point in zooplankton data along a pH gradient that minimizes the residual errors to the two group means. This split represents the step in the step function model and the pH of maximal zooplankton community change along the acidity gradient.

Objective 4

The step in the step function was used as the threshold pH at which the zooplankton community changes from an "undamaged" to a "damaged" community state. The steps were compared between the geographically and morphometrically corrected and uncorrected models and the species richness and abundance models. The selection of the pH at the step in the step function as our threshold was our objective approach to the value-laden component of threshold selection. Arguably, it represents an extremely nonconservative, i.e., nonprotective, value set, as the step is positioned at a pH at which half of the change in community composition associated with pH has already occurred.

Because of the lack of comparable data sets, i.e., with monthly samples over the ice-free season, validation of this threshold was not possible, nor do we particularly expect all regions to have the same threshold. However, we did compare the results of the model with a recent zooplankton survey conducted in Killarney Provincial Park, Ontario (Holt and Yan 2003). Each lake in this survey was visited once in the summer of 2000, and a composite zooplankton sample was generated from three vertical hauls at one open-water station. Fifteen lakes in this study fell within the pH range of the data set analyzed herein. The pH thresholds for zooplankton species abundances based on CA scores and for species richness were identified in this Killarney Park data set using the step function model described above.

Results

The average crustacean species richness varied from 4.3 to 12.3 (mean = 8.5) in the 47 study lakes. Species richness was highly correlated with acidity and morphometric factors (Table 1). The CA ordination of logged species abundances explained 58% of the total variance in zooplankton in the first four axes (Fig. 1). The first axis, explaining 24% of variance, was most highly correlated with acidity and morphometric factors (Table 1). The differences in CA scores between our study and that of Yan et al. (1996) can be explained by our count data transformations.

Geographic patterns were evident for species abundances (Mantel test, $r_M = 0.14$, $p = 0.01$), though not for species richness ($r_M = 0.06$, $p > 0.05$). However, in the multiple regression, species richness was significantly predicted from latitude, the cube of longitude, and log of lake volume (Table 2). Zooplankton species abundances based on CA scores were significantly predicted from latitude, the cube of longitude, and mean depth, with 53% of variance explained in the first four axes of CCA (Table 2). Because of these spatial and morphometric influences on zooplankton, the relationship between acidity and zooplankton communities is potentially confounded. Although zooplankton communities may be responding to pH, they may alternatively be responding to other geographical or morphometric factors that covary with pH.

The variance in species richness and species abundances attributable to spatial and morphometric factors was removed leaving spatially and morphometrically "corrected" community data. Hereafter we will refer to these data simply as "corrected data".

The relationship between the corrected zooplankton data and acidity was modeled with both linear and step functions (Fig. 2). Species richness and the first CA axis (the axis which was best correlated with acidity, $r = -0.67$, $p < 0.001$) were the community metrics modeled, with one exception. For the morphometrically corrected species abundances, we used the second CA axis because it was more highly correlated with acidity ($r = 0.57$, $p < 0.001$). The fit of the linear and step function models were not significantly different (F test, $p > 0.05$), indicating that both provide equally accurate pattern descriptions; however, we selected the step function model for further analyses because, unlike the linear model, it objectively identified a step, which we could use as a threshold in the corrected zooplankton data.

The split point identified by regression tree analysis (pH 6) represents the pH that divided the zooplankton community data into two groups with the lowest sum of squared

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Table 1. Pearson's product–moment correlation coefficients between physical and chemical variables and correspondence analysis (CA) axes of logged species abundances and species richness.

CA axis 1		CA axis 2		CA axis 3		CA axis 4		Species richness	
Variable	r	Variable	r	Variable	r	Variable	r	Variable	r
pH	–0.66	DOC	–0.53	SO_4	–0.4	pH	0.56	pH	0.70
log Alk	–0.52	Secchi	0.43	Al	0.34	log Alk	0.53	log Alk	0.54
SO_4	–0.53	Chl *a*	–0.32	Ca	0.52	C_B	0.53	SO_4	0.41
C_B	–0.44	log TP	–0.36			Ca	0.57	C_B	0.56
Al	0.57							Al	–0.52
Ca	–0.49							Ca	0.57
DOC	0.44							log A_0	0.45
Secchi	–0.49							log V	0.52
Chl *a*	0.42							z	0.47
TN	0.38							z_{max}	0.47
log TP	0.59								
log A_0	–0.61								
log V	–0.74								
z	–0.79								
z_{max}	0.78								

Note: All variables with significant correlations at $p < 0.05$ ($n = 47$ lakes) are included. Variables include aluminum (Al), calcium (Ca), dissolved organic carbon (DOC), chlorophyll *a* (chl *a*), total phosphorus (TP) and nitrogen (TN), alkalinity (Alk), sum of base cations (C_B), lake area (A_0), lake volume (V), mean depth (z), and maximum depth (z_{max}).

errors (SSE) in the group means. In a plot of SSEs for all possible splits in the zooplankton data, there is a narrow and deep trough at the selected step in pH (Fig. 3). This indicates that the splits selected for each model represent the most accurate choices of thresholds.

The choice of pH 6 was not an artifact of decreased error associated with a midpoint split. To test for this possible artifact, we truncated the pH gradient in four different ways: from 5–7 to 5.5–7, 5.7–7, 5–6.3, and 5–6.5. In each case, the same pH 5.98 threshold was identified.

The step in the step function reflects a shift in species abundances. *Daphnia dubia* and *Sida crystallina* were only found at pH > 6. The relative abundances of *Daphnia mendotae*, *Cyclops bicuspidatus thomasi*, and *Eubosmina longispina* were much higher at pH > 6 (Fig. 4). In contrast, the abundances of *Leptodiaptomus minutus* and *Bosmina longirostris* were higher in lakes of pH < 6.

Changes in the relative abundances of higher-order taxonomic grouping than species were also evident at the pH 6 threshold. The relative abundance of anomopods decreased significantly in lakes of pH < 6 compared with lakes of pH > 6 (from 26 to 20% mean abundance, $p < 0.05$), primarily because of declines in *Daphnia* spp. Relative abundances of mature calanoid copepods were marginally higher in lakes with pH < 6 (28 vs. 20%, $p = 0.07$). Mature cyclopoid copepods and ctenopod abundances were similar across the entire pH range.

The models based on corrected and uncorrected data yielded similar pH thresholds of approximately 6 (Table 3). Though patterns in zooplankton communities related to spatial and morphometric factors did exist, these factors did not greatly influence the relationship between zooplankton and acidity in terms of the identification of a threshold. Hence, the uncorrected data were used for further analysis.

The species richness and species abundance models yielded similar thresholds. For the purpose of selecting thresholds of community change, the extra information provided by species abundances did not alter targets provided by species counts.

The pH thresholds from the 15 Killarney Park lakes were similar to those identified in this study from Muskoka–Haliburton (Fig. 5). A pH threshold of 6.15 was identified for changes in CA axis 1 scores based on species abundances. A pH threshold of 5.8 was identified for changes in species richness.

Discussion

A pH of 6 was the point of maximal community change along the acidity gradient in this data set. Where thresholds are needed for management of lake acidification, this pH can be used to distinguish damaged and undamaged communities. In comparison with previously identified thresholds, this one has the potential disadvantage of being very nonconservative. However, it has the advantages of being community-based, sensitive to species abundances as well as occurrences, unaffected by morphometry and geography, and objectively identified. Nonetheless, it is possible that other factors, aside from morphometry and geography, may have confounded our endpoint selection. Possibilities include (*i*) geographic factors other than those we considered, e.g., watershed linkages, (*ii*) chemical variables other than pH that are correlated with zooplankton community structure, (*iii*) quantity and quality of the zooplankton food resource, and (*iv*) altered predation regimes. We consider each of these additional complications below, but conclude that pH 6 can be still be used as a reliable threshold of zooplankton community change with acidification in south-central Ontario as long as the value that this threshold represents is understood, i.e., an appreciable amount of community change is acceptable.

Because the lakes are located in five tertiary watersheds (Cox 1978), it is possible that dispersal of zooplankton colonists over the landscape may have influenced community

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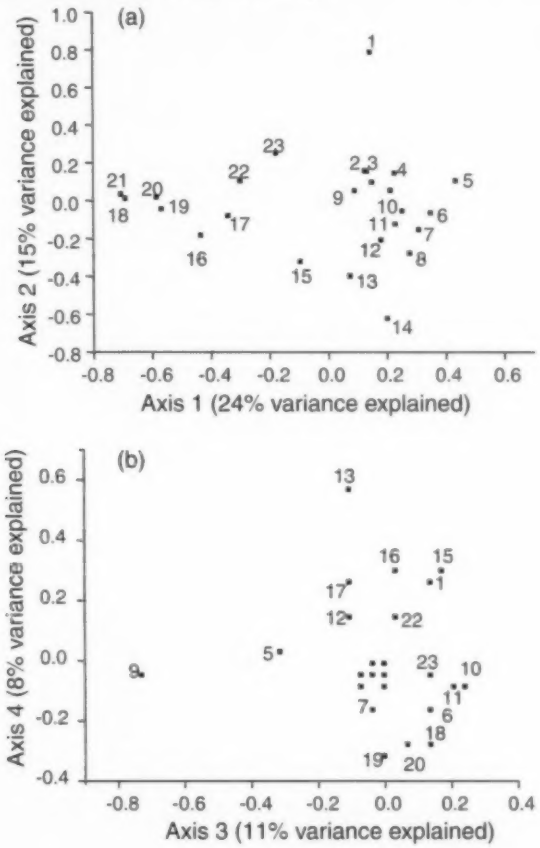
Fig. 1. Species scores of correspondence analysis of logged zooplankton species abundances from 47 Dorset study lakes: (*a*) first and second axes and (*b*) third and fourth axes. 1, *Daphnia pulex*; 2, *Leptodiaptomus minutus*; 3, *Holopedium gibberum*; 4, *Orthocyclops modestus*; 5, *Daphnia ambigua*; 6, *Alona* spp.; 7, *Ceriodaphnia* spp.; 8, *Diaphanosoma* spp.; 9, *Neobosmina tubicen*; 10, *Bosmina longirostris*; 11, *Tropocyclops* spp.; 12, *Cyclops vernalis*; 13, *Chydorus sphaericus*; 14, *Daphnia retrocurva*; 15, *Skistodiaptomus oregonensis*; 16, *Daphnia mendotae*; 17, *Cyclops bicuspidatus thomasi*; 18, *Daphnia dubia*; 19, *Daphnia longiremis*; 20, *Sida crystallina*; 21, *Eubosmina longispina*; 22, *Epischura lacustris*; 23, *Cyclops scutifer*.



structure and thus confounded our endpoint selection. However, there was no significant difference in CA scores among the five watersheds (analysis of variance (ANOVA), $p > 0.05$). One of the watersheds did have a higher species richness than the other four (ANOVA, $p < 0.05$); however, this watershed contained only three lakes, and their removal did not alter the pH threshold in the step function model. Hence, any watershed-scale compositional influences were minor and can be ignored.

Zooplankton are influenced by several water quality parameters in addition to pH, but they do not appear to have influenced our thresholds. Interlake differences in aluminum (Al) probably did not affect our thresholds. Monomeric Al is toxic to zooplankton at high concentrations, though this effect is dwarfed by acidity in Canadian Shield lakes (Havens 1992; Havens et al. 1993). The total Al concentrations in our study lakes ranged from 9 to 136 $\mu g \cdot L^{-1}$, below the lethal zooplankton concentrations identified in previous studies (Havas 1985, 1992). Further, Al concentrations were weakly correlated with zooplankton community structure in comparison with pH, and the correlation of Al with dissolved organic carbon ($r = 0.67$, $p < 0.001$) suggests that most Al was likely in nontoxic organic complexes (Driscoll et al. 1980) where levels were high. It is therefore unlikely that Al is an

Table 2. Model parameters and percent variance explained for (*a*) linear regression predicting species richness and (*b*) canonical correspondence analysis (CCA) explaining species abundances based on geographic and morphometric factors.

(*a*) Linear regression predicting species richness.

Independent variable	Coefficient	*p* value	r^2
Latitude	–0.37	0.009	0.18
Longitude^3	–0.28	0.04	
log lake volume	1.39	0.0001	0.28

(*b*) CCA explaining species abundances.

Independent variable	*p* value	% variance explained
Longitude^3	0.001	11
Latitude	0.09	
Mean depth	0.005	15.9

Fig. 2. Step function plots modeling the relationship between both (*a*) species richness and (*b*) species abundances based on correspondence analysis (CA) scores and pH (n = 47 lakes).

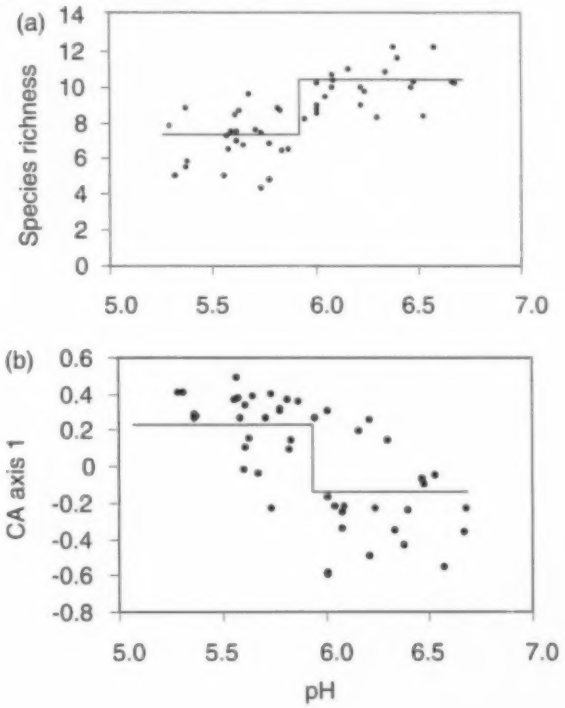


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Fig. 3. Sum of squared errors (SSE) associated with all splits in the (*a*) species composition data (correspondence analysis (CA) scores) and (*b*) species richness data along a pH gradient. The minimum represents the split in the zooplankton community data.

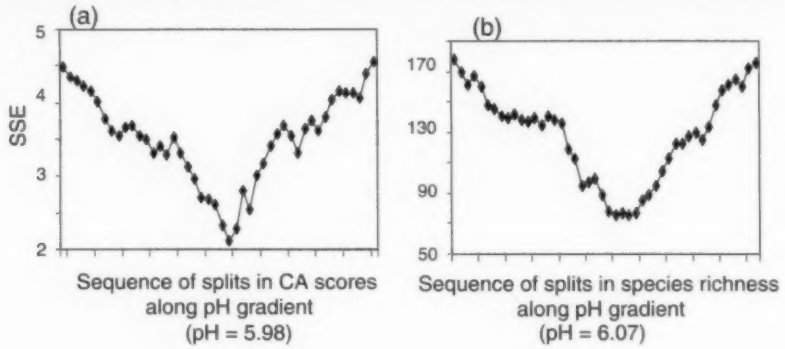

Fig. 4. Changes in species percent abundances between lakes of pH < 6 (solid bars) and pH > 6 (open bars) (n = 47). All differences are significant (t tests and Mann–Whitney U tests, $p < 0.05$).

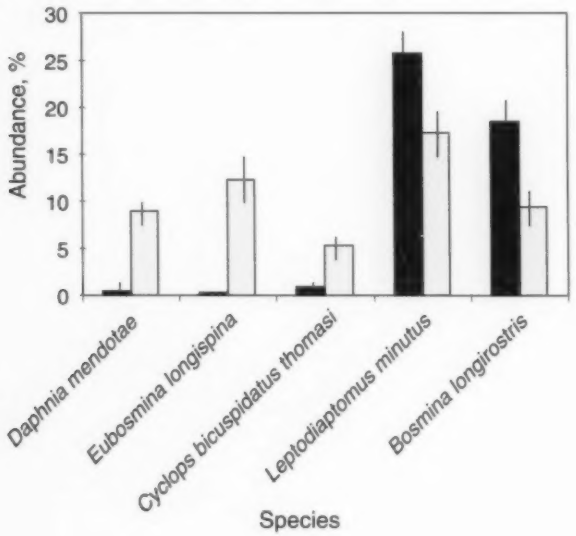

Table 3. Thresholds in zooplankton species richness and species abundances along a pH gradient based on regression tree analysis.

	pH threshold	
	Species richness	Species abundances
Uncorrected	5.98	5.98
Geographically corrected	6.07	5.98
Morphometrically corrected	6.07	6.03

Note: These thresholds represent the split of the data into two groups along a pH gradient that minimizes the mean squared error (MSE) of the step function model.

important regulator of zooplankton community change in this data set.

Calcium may influence zooplankton communities by protecting against the harmful effects of H^+ and Al (Havas 1985). However, interlake differences in Ca probably did not influence our threshold. Ca concentrations in all lakes exceeded the minimum needs of Ca-rich taxa (Alstad et al. 1999). In addition, the Ca concentrations were lower than those thresholds at which hard-water communities emerge (Tessier and Horowitz 1990). In previous North American regional studies of softwater lakes, Ca was not an important predictor of zooplankton species composition (Siegfried and Sutherland 1992; Havens et al. 1993; Yan et al. 1996). In our study, the correlations of zooplankton species richness and abundances with Ca were weaker than those with pH, and Ca itself was highly correlated with pH (r = 0.77, $p < 0.01$).

Zooplankton communities change with nutrient enrichment (Brezonik et al. 1984), but any such influence probably did not influence the relationship between zooplankton and acidity in our lakes. Nutrients may be correlated with zooplankton biomass (Yan 1986; Siegfried and Sutherland 1992) and species composition (Sarvala and Halsinaho 1990; Yan et al. 1996). However, in our study, DOC, Secchi depth, TP, and total nitrogen concentration (TN) were more strongly correlated with different community attributes (i.e., CA axis 2) than those related to pH. Of these variables, DOC, Secchi depth, and TP were significantly correlated with mean lake depth ($p < 0.05$). Shallower lakes were more nutrient rich. The variance associated with mean depth did not influence the choice of our acidity threshold; therefore, the chemical variables associated with trophic status did not influence the determination of our threshold.

The abundance and size structure of zooplankton communities are influenced by predators (Brooks and Dodson 1965; Yan et al. 2001). Among the most significant invertebrate predators in temperate lakes, including acidic lakes (Yan et al. 1991), is the acid-tolerant phantom midge, *Chaoborus* spp. In our study lakes, the abundance of *Chaoborus* varied widely (0–870 individuals·m^{-2}, Persaud and Yan 2001), implying that invertebrate predation pressure also varied widely among lakes. Both species richness and species abundances (CA scores) were correlated with the log of *Chaoborus* abundance (r = –0.50 and 0.55, respectively, $p < 0.001$). To identify patterns unconfounded by *Chaoborus* abundances, the associated variance was removed from the species rich-

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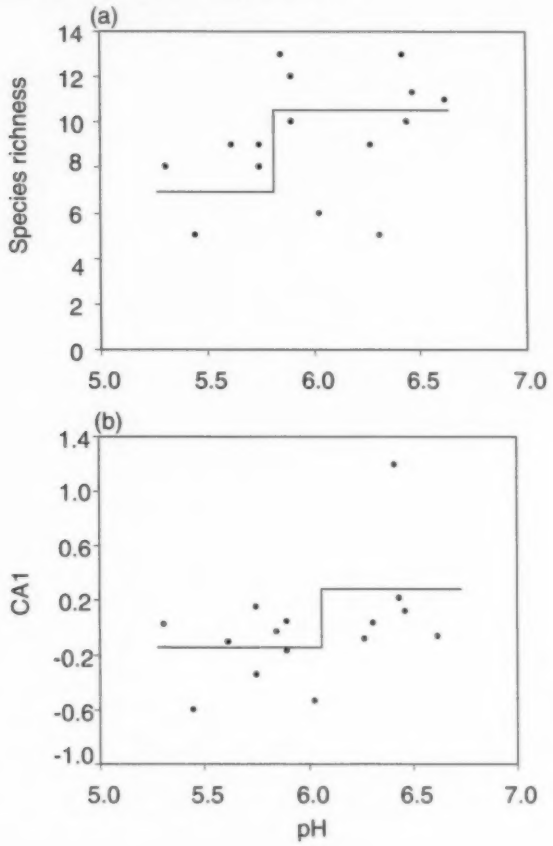
Fig. 5. pH thresholds for (*a*) correspondence analysis (CA) scores based on species abundances (pH 6.15) and (*b*) species richness (pH 5.8) for 15 zooplankton communities of lakes in Killarney Park, Ontario, sampled in 2000.



ness and species abundance data, using the same methods as in objective 2. The pH thresholds identified from the zooplankton data corrected for *Chaoborus* abundances did not differ from the uncorrected data, suggesting that *Chaoborus* abundances did not affect our endpoint selection.

The role of fish predation in controlling zooplankton communities is widely recognized. In one experimentally manipulated lake with no piscivores, the addition of bass caused a decrease in planktivore abundances and a shift in zooplankton species composition to larger bodied cladocerans (Yan et al. 2001). In the present study, three of the 47 lakes do not contain fish. When these lakes were removed from the regression tree analysis, the same pH thresholds resulted. The presence of fish therefore did not influence the relationship between zooplankton communities and acidity in the choice of a threshold. It is possible that differences in fish planktivore abundances among lakes may have influenced zooplankton communities; however, no data were available to test this prediction.

We acknowledged at the outset that thresholds selected should vary among regions and with desired levels of community protection. Nonetheless, previous studies have, on several occasions, identified similar pH thresholds to ours, (i.e., near 6) in zooplankton community data, though they have done so subjectively (Kelso et al. 1986; Locke and Sprules 1993). However, there are a few examples of lower pH thresholds. Sprules (1975*a*) and Keller (1981), working in heavily impacted Sudbury-area lakes, both identified a threshold at pH 5. The lakes used in these studies had a longer, more acidic pH gradient (pH 3.8–7.0) than those of other studies and included far more low-pH lakes. This inclusion of more acidic lakes may have lead to more extreme damage of zooplankton communities and a lower selected threshold.

Using the threshold of pH 6 to distinguish between damaged and undamaged ecosystems suggests that significant damage has occurred in Ontario. Neary et al. (1990) estimated that 19 000 lakes in Ontario had a pH < 6 in 1990, primarily as a result of anthropogenic acid deposition. However, the number of damaged zooplankton communities may exceed this estimate, depending on how thresholds of damage are identified. We estimated the point along a pH gradient which best divided the lakes into two community types. This means that half of the total change in community composition that can be attributed to pH occurs above pH 6. Therefore, a threshold of pH 6 is not conservative from the standpoint of protection of zooplankton communities. Nonetheless, we feel that it is a rational threshold to use because it is community-based, sensitive to species abundances as well as species occurrences, unconfounded by spatial and morphometric factors, and objectively identified. Further, it represents a pH at which community composition changes most rapidly along the acidity gradient.

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Optimal effort controls for the multispecies groundfish complex in New England: what might have been

Daniel S. Holland and Jean-Jacques Maguire

Abstract: Age-structured models are used to calculate catches and revenues of the principal stocks in the northeast multispecies groundfish fishery over the 1982–1997 period assuming alternative control rules on fishing effort had been employed. Various static levels of nominal effort are compared with controls that maintain fishing mortality below overfishing thresholds for all stocks. An unambiguous result from this analysis is that substantial reductions in fishing effort would have increased the value of the fishery even if resulting increases in spawning stock biomass (SSB) had not increased recruitment. Simple controls on nominal effort designed to maximize revenues would have provided nearly equivalent revenues to those achieved by maintaining fishing mortality for each stock at its individual maximum sustainable yield (F_{MSY}) but would have led to overfishing of some stocks. Without the ability to tune the relative catches across stocks, strict controls on effort designed to prevent overfishing on individual stocks would likely have resulted in significantly lower and more variable revenues. Achieving SSB targets for three stocks would not have been possible given the observed recruitment.

Résumé : Nous avons utilisé des modèles structurés d'après l'âge pour calculer les prises et les revenus des principaux stocks de la pêche commerciale plurispécifique de poissons de fond du Nord-est pour la période 1982–1997, en assumant que des règles de contrôle alternatives de l'effort de pêche avaient été employées. Divers niveaux statiques d'effort nominal ont été comparés aux témoins qui maintiennent la mortalité due à la pêche sous les seuils de surpêche pour tous les stocks. Un résultat clair de cette analyse est que des réductions importantes dans l'effort de pêche auraient augmenté la valeur de la pêche commerciale, même si les augmentations de la biomasse du stock reproducteur qui auraient suivi n'avaient pas fait augmenter le recrutement. Des contrôles simples de l'effort nominal en vue de maximiser les revenus auraient généré presque autant de revenus que ne l'aurait fait le maintien de la mortalité due à la pêche à son F_{MSY} (rendement soutenu maximal) individuel; ils auraient cependant mené à la surpêche de certains stocks. Sans la capacité d'ajuster les captures relatives d'un stock à l'autre, l'utilisation de contrôles stricts de l'effort dans le but de prévenir la surpêche des stocks individuels aurait probablement généré des revenus significativement plus faibles et plus variables. L'atteinte des objectifs relatifs à la biomasse du stock reproducteur pour trois stocks n'aurait pas été possible, avec le recrutement observé.

[Traduit par la Rédaction]

Introduction

The northeast multispecies groundfish fishery prosecuted on Georges Bank, in the Gulf of Maine and southern New England is currently in a rebuilding state after the collapse of several principal stocks in the early 1990s (Northern Demersal and Southern Demersal Working Groups (NDSDWG) 2001). Following the collapse, a variety of management measures were implemented to promote the recovery of the depleted stocks. These include a moratorium on entry, substantial reductions in the number of days that individuals can fish, large year-round and seasonal area closures, and increases in mesh sizes (New England Fishery Management Council (NEFMC) 1996). These measures resulted in significant reductions in fishing mortality on all stocks and many, but not all, are rebuilding (NDSDWG 2001). Despite the recovery trend of the fishery, significant additional reductions in nominal fishing effort may still be required. Legal mandates embodied in the Magnuson–Stevens Fishery Conservation and Management Act require managers to end overfishing on individual stocks and rebuild overfished stocks. Reductions in fishing effort are required if fishing mortality exceeds a threshold (maximum sustainable yield (F_{MSY}) for most stocks) or if stock biomass falls below a threshold. Although fishing mortality is now acceptable or nearly so for several stocks, it is not for others, and spawning stock biomass (SSB) remains well below targets for several stocks (NDSDWG 2001).

Overfishing definitions for each stock are closely related to the fishing mortality expected to produce maximum sustainable yield (Working Group on Re-evaluation of Biologi-

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cal Reference Points for New England groundfish (WGRBR) 2002). However, because only the nominal effort applied to the entire complex is directly managed, it is difficult to maintain fishing mortality at overfishing thresholds for all stocks simultaneously. In a mixed fishery, eliminating overfishing on all stocks may require reducing fishing mortality far below targets for some stocks, thereby reducing revenues for the overall complex. Alternatively, setting fishing effort to maximize sustainable revenues for the overall complex will almost certainly result in overfishing of some stocks in some years. Although this conundrum, requiring balancing of economic and biological risks, has long been recognized (e.g., Larkin 1977), the U.S. continues to address it in an ad hoc fashion rather than develop an explicit framework for assessing and evaluating the trade-offs necessary.

This paper uses a type of retrospective analysis to assess alternative control rules on fishing effort for the overall northeast multispecies groundfish fishery. Various static levels of nominal effort are compared with controls that keep fishing mortality at or below overfishing thresholds for all stocks. Overfishing thresholds are the fishing mortality rates consistent with F_{MSY} (WGRBR 2002). Simulations are also run with nominal effort set separately for each stock to maintain F_{MSY} for that stock. Although the means to tune relative fishing mortality across stocks is limited in reality, this scenario provides a benchmark to compare outcomes from more feasible management scenarios. Trade-offs between economic and biological risks are discussed in light of these modeling results.

This analysis complements an earlier study by Overholtz et al. (1995), in which effort controls were simulated on a subset of these stocks but the annual and interstock variation in fishing mortality and ramifications for eliminating overfishing on individual stocks were not considered. This analysis also differs from the Overholtz et al. (1995) analysis in that it looks at what could have occurred in the past using observed recruitment rather than predicting recruitment using a parametric stock–recruitment function. Parametric recruitment is, however, considered in a sensitivity analysis.

Methods

A bioeconomic model is used to simulate stock sizes, harvests, and revenues from 1982 to 1997 assuming the observed recruitment and relative catchability of stocks as estimated by virtual population analysis (VPA) but allowing for alternative levels of nominal fishing effort. Data for the simulations were derived from published VPA assessments conducted by the Northeast Fisheries Science Center. VPA assessments were not available beyond 1997 for several stocks, thus it was not possible to model the entire complex of stocks as a system beyond that point and simulations were curtailed there. The analysis employs age-structured models of 10 New England groundfish stocks. These include the Georges Bank cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), winter flounder (*Pleuronectes americanus*), and yellowtail flounder (*Limanda ferruginea*) stocks, the Gulf of Maine cod stock, the southern New England winter flounder and yellowtail flounder stocks, the Cape Cod yellowtail flounder stock, and the Gulf of Maine – Georges Bank witch flounder (*Gyptocephalus cynoglossus*) and American plaice (*Hippoglossoides platessoides*) stocks. For all stocks other than Cape Cod yellowtail flounder, the model is initialized with the 1982 numbers-at-age from the published VPA based assessments for each stock. The Cape Cod yellowtail stock is modeled only from 1985 forward because the assessment for that stock only goes back to 1985. The number of age-1 fish in all years modeled corresponds with the observed recruitment reported in the latest available stock assessments. For age 2 and above, the number of individuals (N) of stock i and age j in year t is endogenous to the model

$$(1) \qquad N_{i,j+1,t+1} = N_{i,j,t}\, e^{-Z_{i,j,t}} \; \forall \; j \neq 1$$

Following Overholtz et al. (1995), cohorts are tracked through age 15, after which the survival rate is assumed to be zero. Total mortality for each cohort in each stock ($Z_{i,j,t}$) is the sum of fishing and natural mortality. Consistent with the VPA assessment for each stock, natural mortality is set at an instantaneous rate of 0.20 for all stocks except witch flounder, which is 0.15. Cohort and species specific fishing mortality is calculated as

$$(2) \qquad F'_{i,j,t} = F^0_{i,j,t} E_{i,t}$$

where $F^0_{i,j,t}$ are the age-specific fishing mortalities reported in the VPA assessments for each stock and $E_{i,t}$ is a scalar used to multiply the matrix of fishing mortalities for each stock (these are available from the authors upon request). By denominating effort simply as a proportion of the observed level, we avoid the necessity of defining a cardinal scale for nominal effort. However, the implicit assumption made is that nominal effort is measurable and controllable and is linearly related to fishing mortality. We assume that the fishermen's targeting and the resulting relative catchability of the different cohorts and stocks would have remained the same regardless of nominal fishing effort but that reductions in total days fished in the groundfish fishery would have resulted in independent and proportionate reductions in fishing mortality by age and species. Although it would be an imperfect control, reductions of nominal effort might be accomplished by limiting the number of days fished, in which case we would define $E_{i,t}$ as the ratio of modeled days fished to observed days fished by vessels targeting groundfish.

The relative catchability of different stocks after 1993 was heavily influenced by a complex and changing set of regulations that confounds the assessment of simple effort controls. Consequently, the model employs the average relative catchability during the 1990–1993 period to transform nominal effort into fishing mortality for the 1994–1997 period. The average fishing mortality by species and age for that 3-year period is scaled by $E_{i,t}$. Here the implicit assumption is that targeting patterns from 1994 to 1997 would have remained similar to those observed in the prior 3 years had the other regulatory measures not been imposed.

Three alterative scenarios are investigated. Scenario 1 assumes that nominal effort is held constant for the overall complex over the entire period such that $E_{i,t}$ is equal for all stocks i and years t. The relative mortality of each stock and cohort correspond directly with the VPA assessments of each stock. A full range of values for the effort scalar is investigated.

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Scenario 2 assumes only overall nominal effort is controlled, but $E_{i,t}$ is adjusted downward each year to the extent required to maintain fishing mortality at or below thresholds (Table 1) for all stocks. $E_{i,t}$ are constrained to be equal for all stocks in a given year but may vary over time. Consequently fishing morality for some stocks may be set well below thresholds in some or all years, but overfishing (according to legal definitions) does not occur for any stock. The controls on overfishing are based on fully recruited fishing mortality for all stocks except Georges Bank winter flounder for which the overfishing threshold is based on biomass-weighted fishing mortality (an average of fishing mortality across ages weighted by biomass-at-age).

Scenario 3 adjusts the effort scalar for each stock in each year to achieve the target fishing mortality that corresponds with F_{MSY}. As with the previous scenarios, the prescaled matrices $F^0_{i,t}$ of partial recruitment for each stock corresponds with the VPA, but each $E_{i,t}$ is determined independently.

The Baranov catch equation is used to calculate catch as

$$(3) \qquad C_{i,j,t} = N_{i,j,t}\frac{F'_{i,j,t}}{Z_{i,j,t}}(1 - e^{-Z_{i,j,t}})$$

where $C_{i,j,t}$ is the catch in numbers from the ith stock and jth cohort. Harvest weight ($Y_{i,j,t}$) from each cohort for each stock is calculated by multiplying numbers of individuals caught by their age-specific weights ($W_{i,j,t}$), which are the observed catch-weights-at-age reported in the stock assessments for each stock.

$$(4) \qquad Y_{i,j,t} = C_{i,j,t}W_{i,j,t}$$

For older cohorts, for which weight-at-age is not reported in the assessment, published Von Bertalanffy equations (NEFMC 1996) and length–weight relationships are used to calculate weight-at-age.

Annual revenues for each stock are calculated using projected catches and prices for each stock and cohort

$$(5) \qquad R_t = \sum_{i=1}^{10}\sum_{j=1}^{15} P_{i,j,t}Y_{i,j,t}$$

where $P_{i,j,t}$ is the species and market category specific price associated with that stock and cohort. As described in Appendix A, these prices are determined endogenously by the model as a function of annual projected catches aggregated by species and market category and a time trend. For the purpose of predicting and assigning prices, catches from different stocks of the same species and from different cohorts are grouped into the market category into which each cohort falls based on the average weight-at-age for that stock and the cull used by the Portland Fish Exchange (see Table A1). Because the price models are estimated with prices adjusted to year 2000 values, the projected revenues from the model are in year 2000 US dollars.

To compare the present value of alternative management scenarios, revenues are discounted to 1982 using a discount rate (r) of 0.04

$$(6) \qquad \text{PVR} = \sum_{t=1}^{16}\frac{R_t}{(1+r)^t} + \text{RV}$$

where PVR is the present value (in 1982) of the revenue stream including the value of the residual stock (RV) defined in eq. 7. A higher discount rate of 7% is typically used for cost–benefit analysis of regulatory actions. However, following Overholtz et al. (1995), a 4% discount rate is used because inflation is already removed from projected prices by estimating price models with deflated prices. Different management policies leave different biomasses of varying age structures at the end of the simulation policy, and it is important to consider the value of this residual stock. Thus, the value of the residual stock in 1997 is calculated and added to the discounted revenue stream projections from the 1982–1997 period. The residual value is calculated by running the model forward with no added recruitment assuming the 1997 fishing mortality vector until the residual stock is depleted. Annual yields are multiplied by 1997 prices and discounted to 1982.

$$(7) \qquad \text{RV} = \sum_{t=17}^{32}\sum_{i=1}^{10}\sum_{j=1}^{15}\frac{P_{i,j,1997}Y_{i,j,t}}{(1+r)^t}$$

Prices from 1997 are used to estimate residual value because the harvest quantities in the residual yield projections are much lower than what would be projected if the model continued to add recruits. This would tend to unduly inflate price projections. The assumption is made that prices in the final year of the simulation are indicative of prices that would be expected to prevail if the same harvest strategy were continued in subsequent years.

Sensitivity analysis

The main results of the model are based on the assumption that the relative catchability of species and age classes and the magnitude of recruitment would have been unaffected by changes in nominal fishing effort. We explore the sensitivity of the model by relaxing these assumptions. We allow the pattern of fishing mortality across species and ages to vary stochastically by drawing with replacement annual fishing mortality patterns from the observed set. For each year modeled, an entire matrix of fishing mortality-at-age by species, F^0_t, is drawn from the observed 1982–1993 time series. Fishing mortality vectors are not drawn independently for each stock as that would allow relatively high mortality rates on all stocks at once, whereas the observed patterns, which are based on relatively constant total nominal effort, represent a shifting of effort among stocks. The average value of F^0_t is used to calculate the value of the residual stock.

We also allow for parametric recruitment in place of observed recruitment. Beverton–Holt recruitment functions estimated by the working group on reevaluation of biological reference points (WGRBR 2002) are used for this purpose. The working group identified "reasonable" parametric recruitment functions for only 6 of the 10 stocks modeled. These include the Georges Bank cod, haddock, and yellowtail flounder, Gulf of Maine cod, and southern New England winter flounder and yellowtail flounder (Table 1). For the other four stocks modeled in this study, the data did not support the identification of a parametric stock–recruitment relationship. For these stocks, we continue to use the observed recruitment in the sensitivity analysis. We present results

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Table 1. Parameters of Beverton–Holt recruitment functions for the six stocks modeled with parametric recruitment and fully recruited fishing mortality and spawning stock biomass (SSB) targets associated with maximum sustainable yield (WGRBR 2002).

Stock	α	β	σ	F_{MSY}	SSB_{MSY} ($t \times 10^3$)
GB cod	28.285	77.695	0.526	0.18	216.8
GOM cod	9.854	7.516	0.6	0.23	82.8
GB haddock	96.366	187.557	1.326	0.26	250.3
GB yellowtail flounder	90.032	19.84	0.66	0.25	58.8
SNE yellowtail flounder	83.106	18.822	1.201	0.27	45.2
CC yellowtail flounder	NA	NA	NA	0.21	8.4
GB winter flounder	NA	NA	NA	0.32	9.4
SNE winter flounder	47.536	7.398	0.344	0.32	30.1
GOM and GB witch flounder	NA	NA	NA	0.16	19.9
GOM and GB American plaice	NA	NA	NA	0.17	28.6

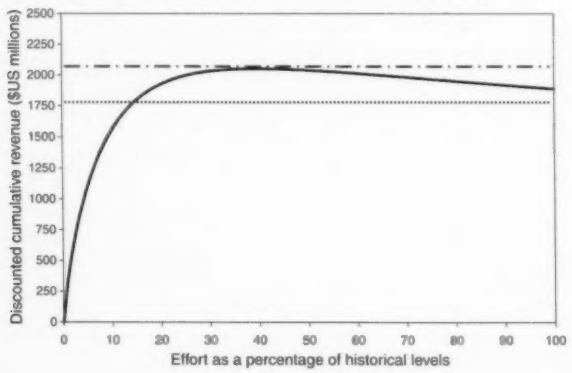
Note: For Georges Bank (GB) winter flounder, the biomass target is total biomass rather than SSB and the fishing mortality target is biomass weighted. NA, not applicable. Stocks: Gulf of Maine (GOM) cod (*Gadus morhua*), Georges Bank (GB) cod, haddock (*Melanogrammus aeglefinus*), yellowtail flounder (*Limanda ferruginea*) and winter flounder (*Pleuronectes americanus*), GOM–GB witch flounder (*Gyptocephalus cynoglossus*) and American plaice (*Hippoglossoides platessoides*), Cape Cod (CC) yellowtail flounder, and southern New England (SNE) yellowtail flounder and winter flounder.

Table 2. The effort, as a percentage of that historically applied, that maximizes the mean present value of revenues (PVR) for 1982–1997 including the discounted value of the residual stock; mean PVR for scenario 1 where the effort scalar is static across years; PVR for scenario 2 where the effort scalar is adjusted each year to the extent needed to avoid exceeding fishing mortality targets for any stock; and the ratio of mean PVR from scenarios 1 and 2.

Sensitivity assumptions	Effort at maximum PVR, scenario 1	Mean PVR, scenario 1 ($US millions)	Mean PVR, scenario 2 ($US millions)	Ratio of PVR scenario 2 to scenario 1
Observed F^0, observed recruitment	0.40	2053	1770	0.86
Observed F^0, deterministic recruitment	0.32	2401	2103	0.88
Resample F^0, observed recruitment	0.41	2066	1733	0.84
Resample F^0, deterministic recruitment	0.33	2400	2096	0.87
Resample F^0, stochastic recruitment	0.38	2557	2228	0.87

Note: Results are shown for the deterministic base model with observed fishing patterns and recruitment, for observed fishing patterns and deterministic parametric recruitment, for resampled fishing patterns and observed recruitment, for resampled fishing patterns and deterministic parametric recruitment, and lastly for resampled fishing patterns and stochastic parametric recruitment.

Fig. 1. Present value of revenues (PVR) for 1982–1997 including the discounted value of the residual stock assuming alternative nominal effort as a percentage of that historically applied for scenario 1 with static effort (heavy solid line). Maximum PVR ($US 1.77 billion) from scenario 2 with nominal effort adjusted each year to eliminate overfishing (thin broken line). PVR ($US 2.08 billion) from scenario 3 with fishing mortality set at F_{MSY} for all stocks in all years (dashed–dotted line).



assuming both deterministic and stochastic recruitment. In the case of deterministic recruitment, the number of age-1 fish for stock i in year $t + 1$ is calculated as

$$(8) \qquad N_{i,1,t+1} = \frac{\alpha S_{i,t}}{\beta + S_{i,t}}$$

where $S_{i,t}$ is the SSB for stock i in year t, measured in thousands of metric tons (t), and $N_{i,1,t+1}$ is measured in millions of recruits. In the case of stochastic recruitment, the deterministic recruitment is scaled by the exponent of a random number with zero mean and a standard deviation equal to that estimated by the working group (Table 2). Recruitment for each stock is limited to the highest observed levels. We run 2000 repetitions (10 000 for stochastic recruitment) of each scenario at each effort level and examine the mean and distribution of outcomes.

Results

The results from scenario 1 indicate that nominal effort corresponding to 40% of that actually applied during the 1982–1997 period would have maximized the present value of fishery revenues with a PVR of $US 2.05 billion (Fig. 1).

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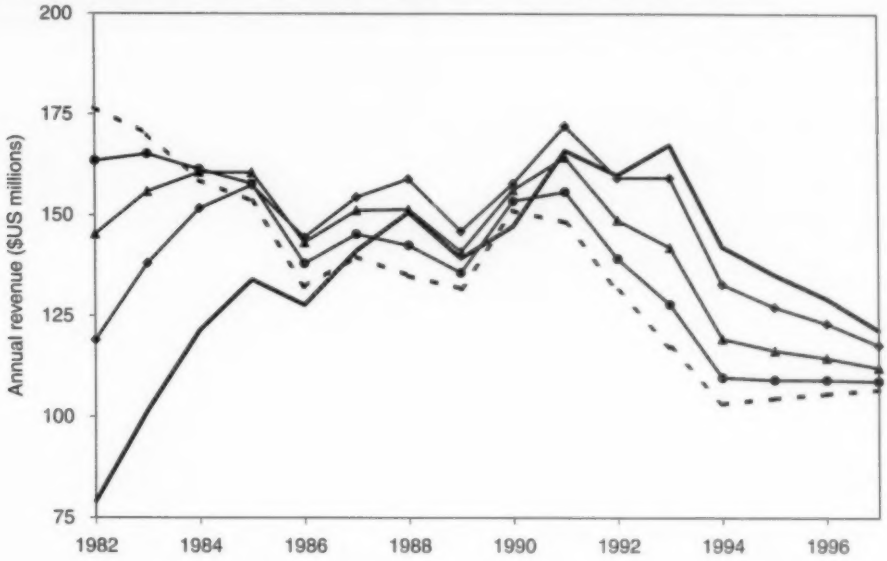
Fig. 2. Annual revenue for the 10-species complex given nominal effort (as a percentage of observed) held constant over time (scenario 1) at 20% (solid line), 40% (diamonds), 60% (triangles), 80% (circles), and 100% (broken line).

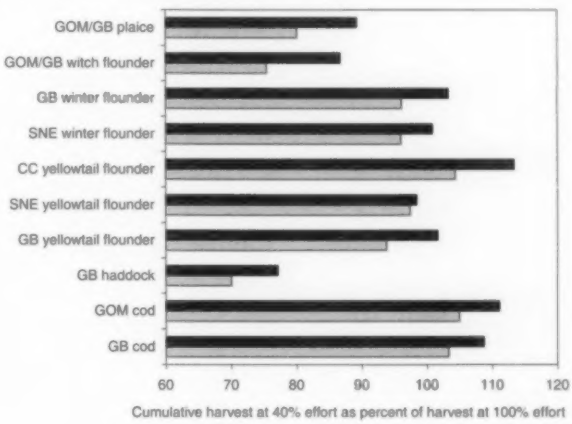


Discounted cumulative revenue for the 1982–1997 period (excluding the value of the residual stock) is maximized at a marginally higher effort level of 46%, but the larger residual stock at the end of the period makes a more conservative policy more valuable. Coincidentally, the undiscounted sum of cumulative revenues (including the value of the residual stock) is also maximized with 60% effort reduction. Relative to no effort reduction, a 60% cut in effort reduces revenue in only the first 3 years. By year 3, revenues are 95% of those associated with no effort reduction, and annual revenues range from 3 to 36% higher in subsequent years (Fig. 2). The PVR with a 60% cut in effort is 9% higher than the PVR with no effort reduction, which equals $US 1.77 billion.

Although a 60% cut in effort maximizes present value of revenues for the overall complex, the changes in total harvest for the period modeled vary greatly across stocks. Harvests from both cod stocks are increased relative to harvests at 100% effort (Fig. 3). However, total harvest falls for several of the flounder stocks and Georges Bank haddock. Harvests from all stocks other than haddock would have increased with more moderate effort reductions in the range of 20 to 30%. Because recruitment is exogenous in these simulations, gains in harvest result purely from increasing yield per recruit by reducing growth overfishing. Relatively greater reductions in effort would have been required to eliminate growth overfishing on the cod stocks and the Cape Cod yellowtail flounder stock than for the other stocks. Thus, given the fixed relative mortalities in scenario 1, maximizing revenue from the cod stocks required sacrificing harvests from several other stocks.

It is informative to compare the potential revenues under simple controls on nominal effort (scenario 1) to those achieved when effort is set independently for each stock (scenario 3). It is unlikely that this could be achieved in practice, but the results provide a benchmark. The maximum

Fig. 3. Cumulative harvest at 40% effort as a percent of cumulative harvest with 100% effort from scenario 1. Comparisons of cumulative harvests with (solid bars) and without (shaded bars) inclusion of the residual harvest are shown for Gulf of Maine (GOM) cod (*Gadus morhua*), Georges Bank (GB) cod, haddock (*Melanogrammus aeglefinus*), yellowtail flounder (*Limanda ferruginea*) and winter flounder (*Pleuronectes americanus*), GOM/GB witch flounder (*Gyptocephalus cynoglossus*) and American plaice (*Hippoglossoides platessoides*), Cape Cod (CC) yellowtail flounder, and southern New England (SNE) yellowtail flounder and winter flounder.



PVR from scenario 1 is 98% of that achieved under scenario 3 when fishing mortality is set equal to F_{MSY} for all stocks in all years (Fig. 1).

However, if it were not possible to adjust relative fishing mortality across stocks, strict adherence to overfishing guidelines (scenario 2) would have required foregoing reve-

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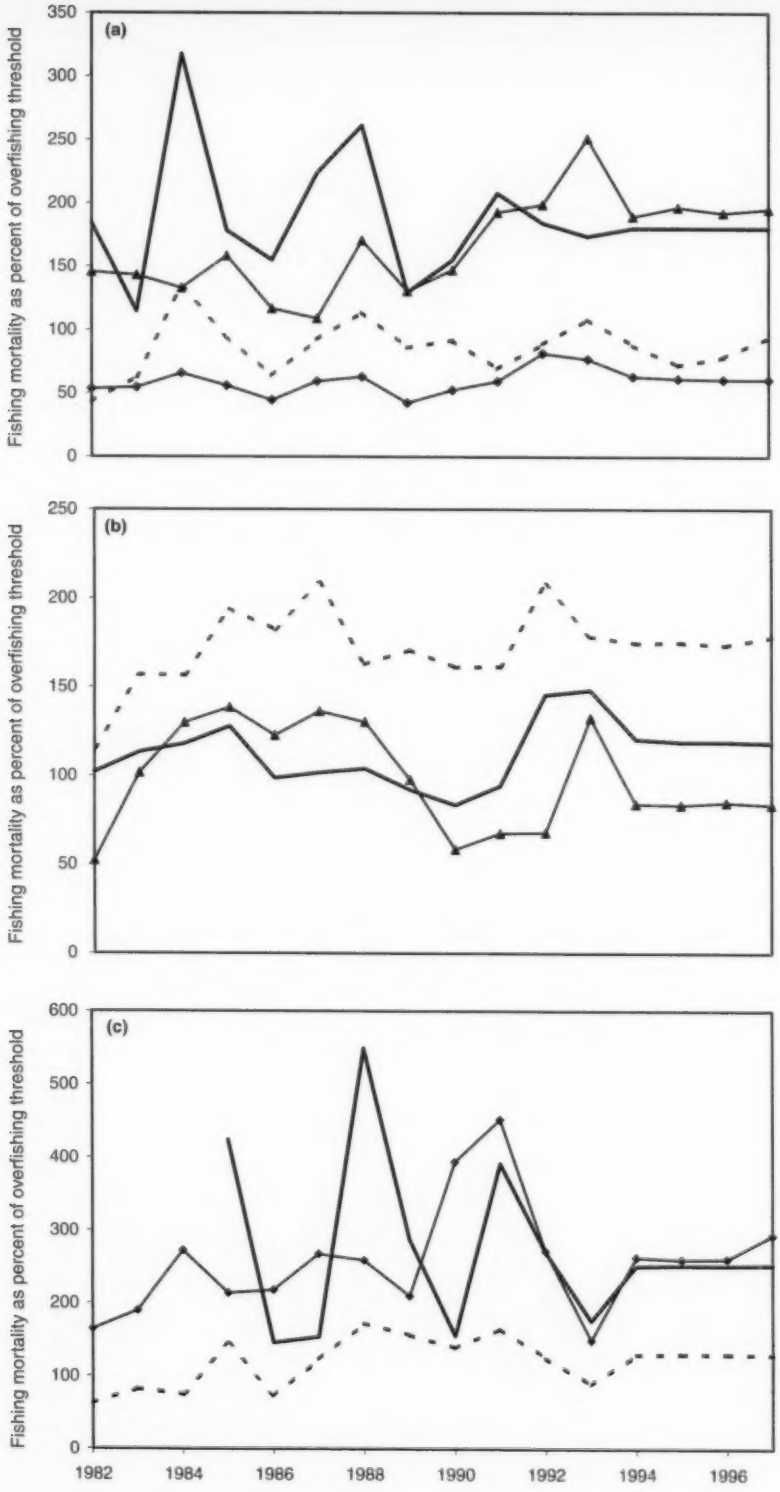

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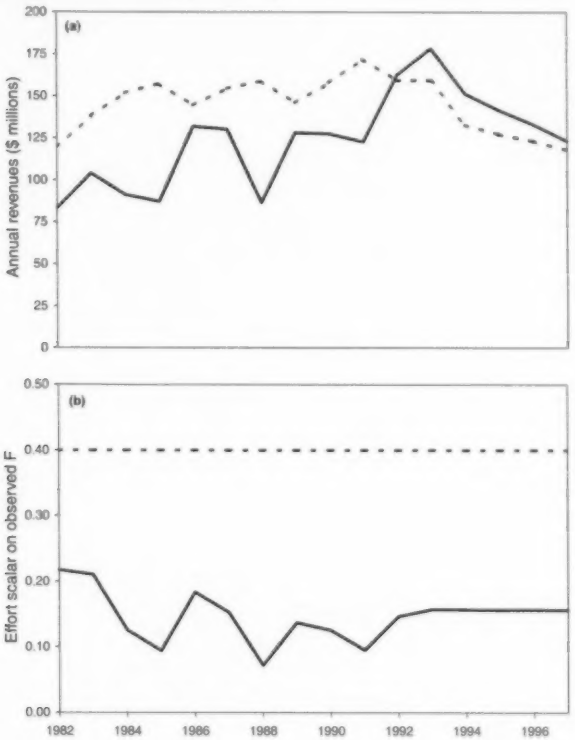
Fig. 4. Fishing mortality as a percentage of the overfishing threshold given constant effort at 40% of observed effort (scenario 1) for (*a*) Georges Bank (GB) cod (*Gadus morhua*) (triangles), haddock (*Melanogrammus aeglefinus*) (diamonds), yellowtail flounder (*Limanda ferruginea*) (solid line), and winter flounder (*Pleuronectes americanus*) (broken line); (*b*) Gulf of Maine (GOM) cod (broken line) and GOM/GB witch flounder (*Gyptocephalus cynoglossus*) (triangles) and American plaice (*Hippoglossoides platessoides*) (solid line); and (*c*) Cape Cod (CC) yellowtail flounder (solid line) and southern New England (SNE) yellowtail flounder (diamonds) and winter flounder (broken line).

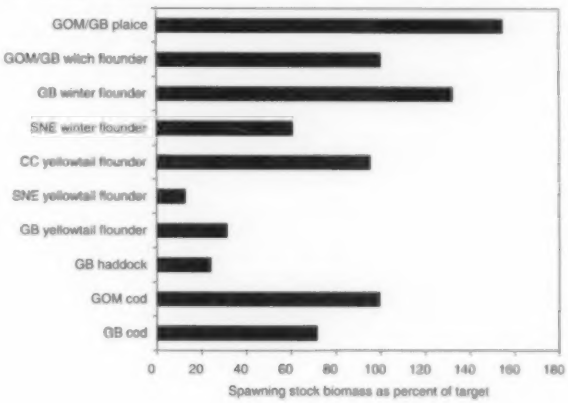
Fig. 5. Comparison of (*a*) annual revenue ($US) and (*b*) annual nominal effort for scenario 1 with 40% of observed effort (broken line) and for scenario 2 with effort adjusted in each year to eliminate overfishing (solid line).



nues to avoid overfishing. For any constant nominal effort, fishing mortality varies greatly both across stocks and over time. This results from a complex combination of factors including changes in age structure and relative availability of different stocks and targeting decisions of fishermen. When nominal effort is held constant at the rate that achieves maximum PVR, the fishing mortality for some stocks fluctuates above and below the overfishing threshold and results in chronic overfishing for many (Figs. 4*a*–4*c*). If only controls on nominal effort are available to managers (scenario 2), strict adherence to overfishing thresholds requires setting effort in any given year at from 7 to 21% of the observed effort levels. This results in a 14% drop in PVR (to $US 1.77 billion) relative to the maximum achieved under scenario 1 (Fig. 1) and results in high variability of nominal effort and revenues from one year to the next (Figs. 5*a* and 5*b*).

The increased variation in revenues under the no-overfishing policy is important from an economic viewpoint. Variation

Fig. 6. Spawning stock biomass (SSB) in 1997 as a percentage of target biomass given nominal effort reductions to eliminate all overfishing (scenario 2) for Gulf of Maine (GOM) cod (*Gadus morhua*), Georges Bank (GB) cod, haddock (*Melanogrammus aeglefinus*), yellowtail flounder (*Limanda ferruginea*), and winter flounder (*Pleuronectes americanus*), GOM/GB witch flounder (*Gyptocephalus cynoglossus*) and American plaice (*Hippoglossoides platessoides*), and Cape Cod (CC) yellowtail flounder and southern New England (SNE) yellowtail flounder and winter flounder. The target is in terms of total biomass for GB winter flounder.



in revenues is undesirable from a socioeconomic standpoint because it increases financial risk and, assuming decreasing marginal utility of income, lowers utility for fishers. Given a downward-sloping demand curve, variation in catches also provides lower total revenues from a given total catch than would be realized with a more even distribution of catches over time. The coefficient of variation (CV) of annual revenues from scenario 2 (CV = 0.224) is nearly twice that of scenario 1 with 40% effort (CV = 0.115). CV in this case is not a measure of uncertainty of model outcomes but rather of variation in revenues. Thus the conservative management strategy designed to reduce biological risk by strict adherence to overfishing definitions can be seen to increase economic risk. This could become particularly important if the precision of stock assessments is low, thereby causing unnecessary economic stresses to the industry.

Although it would have been possible to eliminate overfishing on all stocks with relatively moderate reductions in revenues, it might not have been feasible to rebuild stocks to the target biomass. When effort is restricted to below-overfishing thresholds in all years (scenario 2), SSB for most stocks remains well below targets in 1997 (Fig. 6). Three stocks remain below 50% of the target (southern New England yellowtail at 13% and Georges Bank yellowtail and haddock at 31 and 24%, respectively). It is notable that even

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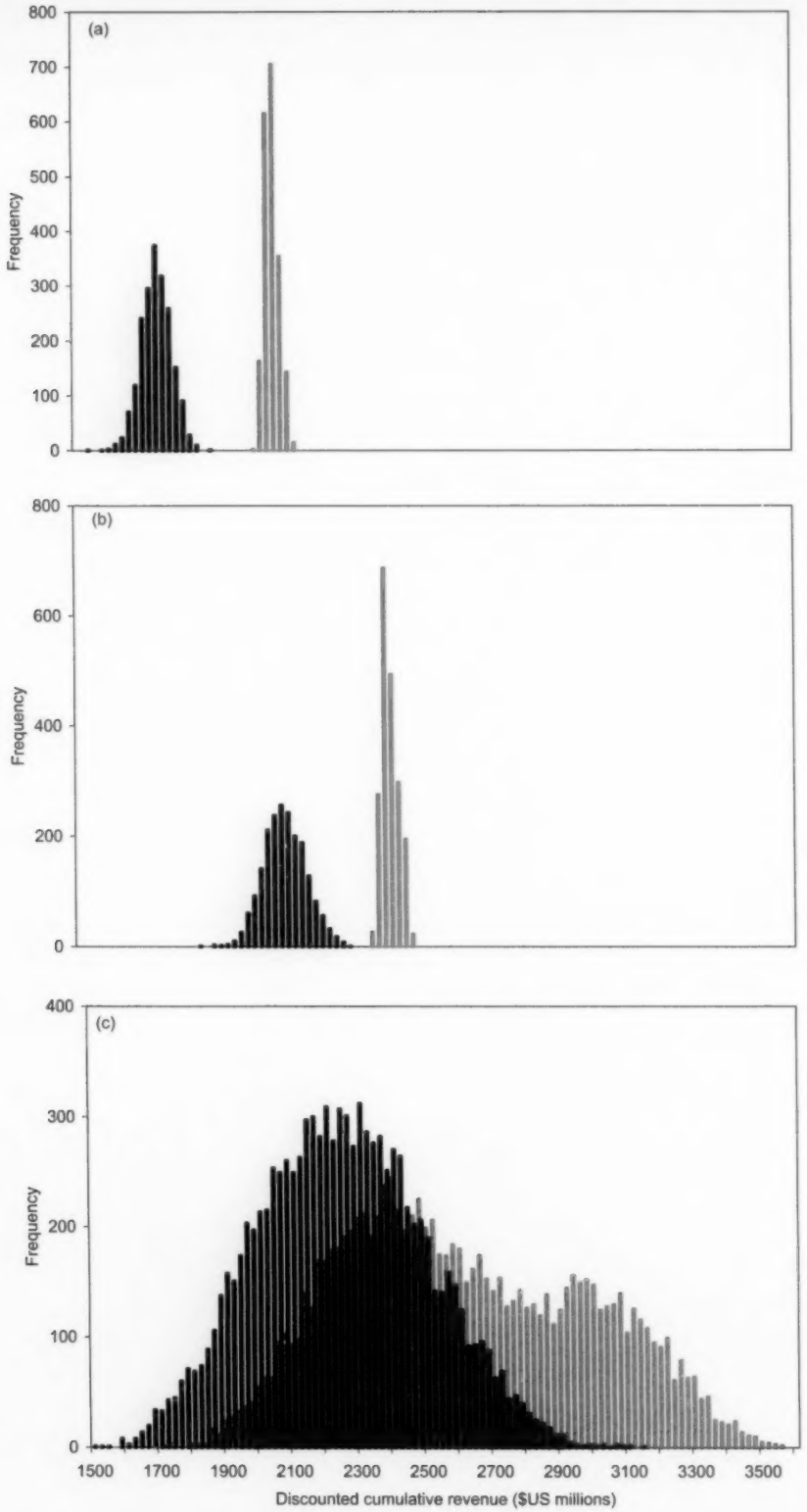

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Fig. 7. Frequency distributions of present value of revenues (PVR) for 1982–1997 including the discounted value of the residual stock from 2000 trials for sensitivity analysis for scenario 1 (shaded bars) and scenario 2 (solid bars) with (*a*) resampled effort and observed recruitment, (*b*) resampled effort and deterministic parametric recruitment, and (*c*) resampled effort and stochastic parametric recruitment.

with a complete cessation of fishing, the SSB of Georges Bank haddock and Georges Bank yellowtail flounder do not rebuild to MSY within the 16-year span modeled as the result of insufficient recruitment over the observed period. Haddock SSB reaches only 30% of the target by 1997.

Sensitivity results

It is uncertain whether and to what extent the projected changes in absolute and relative stocks sizes would have altered targeting behavior and relative fishing mortality rates across cohorts and stocks. Higher stock sizes might also have produced higher recruitment. The sensitivity analysis relaxes the assumptions that observed recruitment and relative fishing mortality would have remained unchanged. Results are presented when either or both of these assumptions are relaxed. The sensitivity analysis suggests that the qualitative results of the base model are relatively robust to these assumptions and relaxing them has predictable impacts.

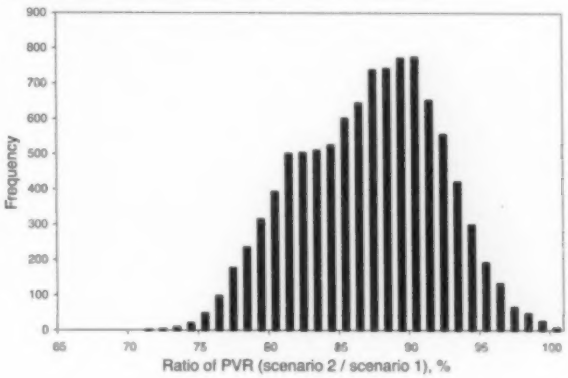
We first consider the case where the historical pattern of fishing effort is maintained but recruitment is assumed to be parametric and deterministic. Relative to the base model, the PVR from scenario 1 (static effort scalar across years) is maximized at a lower effort level, 32% of the historical level. The PVR for both scenarios 1 and 2 is also higher as a result of generally higher recruitment for the six stocks modeled with parametric recruitment. However, the scenario 2 to scenario 1 ratio of maximum PVR, at 88%, is little changed from the base model (Table 2). The PVR for scenario 1 does drop significantly at higher effort levels. With deterministic parametric recruitment, the maximum PVR is 24% higher than that achieved with 100% effort, whereas it was only 9% higher in the base model with observed recruitment.

When fishing patterns are allowed to vary stochastically, but the assumption of observed recruitment is maintained, the results are very similar to those of the base model (Table 2). The effort corresponding with maximum PVR increases slightly to 41%, and the ratio of maximum PVR from scenarios 2 versus 1 declines slightly to 84%. There is variability in outcomes as a result of resampling effort, but the distributions (from 2000 trials) of PVR from scenarios 1 and 2 do not overlap (Fig. 7*a*).

Models with resampled effort and parametric (but deterministic) recruitment generated higher levels of maximum PVR for both scenarios 1 and 2 relative to the base model. However, the scenario 2 to scenario 1 ratio of mean maximum PVR, at 87%, is little changed from the base model (Table 2). Again the distributions of PVR from the two scenarios do not overlap (Fig. 7*b*).

Finally, we consider the case of resampled effort and stochastic parametric recruitment. The variability of outcomes is much higher with stochastic recruitment, so we consider results from 10 000 trials of each scenario and effort level. The mean values of maximum PVR from scenarios 1 and 2 are somewhat higher than those with deterministic recruitment (Table 2). The scenario 2 to scenario 1 ratio of mean PVR from, at 87%, is only a percentage point higher than that of the base model. There is much greater variability in outcomes as a result of highly variable recruitment so that there is some overlap in the distributions of PVR from the two scenarios.

Fig. 8. Frequency distribution of the ratio of maximum PVR from scenario 2 versus scenario 1 with resampled effort and stochastic deterministic recruitment from 10 000 trials.



Although it is convenient to show the distribution of outcomes from the two policies on a single histogram, the histogram suggests a degree of overlap in outcomes we would not actually expect from direct comparison of the two policies because comparisons are being made between trials with different recruitment streams. Relatively low levels of PVR for each scenario correspond with relatively unfavorable recruitment residuals and vice versa. The assumption maintained when the recruitment functions are originally estimated is that the random multiplicative error that scales recruitment up or down from that predicted by the parametric function is uncorrelated with the level of the stock. Thus to compare results of the two policies represented by scenarios 1 and 2, it may be more informative to compare the distribution of the ratio of PVR from the two scenarios when the matrix of recruitment errors is held constant across policies. In each case, the comparison is made on a trial-by-trial basis where the matrix of recruitment errors (not recruitment itself) is held constant. The prescaled fishing mortality pattern F^0 is also held constant across policies for this comparison, though as always the scaling of F^0 varies across policies. The comparison suggests that the probability that PVR from scenario 2 will be higher than that from scenario 1 is extremely low (about one-tenth of a percent). However, the ratio of PVR from the two policies is highly variable, ranging from a low of 69% to a high of 102% (Fig. 8).

The sensitivity analysis with stochastic recruitment also provides some information relevant to assessing the biological risk associated with the two policies. With scenario 1, there is a significant likelihood that SSB for some stocks

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Table 3. Mean spawning stock biomass (SSB) in 1997 as a percent of the target and the percent of trials where the SSB in 1997 was below 50 and 25% of the target.

	Scenario 1			Scenario 2		
		% of trials SSB			% of trials SSB	
Stock	Mean SSB as percent of target	<25% of target	<50% of target	Mean SSB as percent of target	<25% of target	<50% of target
GB cod	64	44	14	146	5	0
GOM cod	63	47	15	145	8	1
GB haddock	116	44	33	167	35	24
GB yellowtail	70	44	23	166	10	2
SNE yellowtail	71	49	37	159	26	16
CC yellowtail*	50	58	3	131	0	0
SNE winter	80	17	1	163	0	0
GB winter*	70	0	0	137	0	0
Witch*	70	0	0	100	0	0
Plaice*	103	0	0	161	0	0

Note: Results are from 10 000 trials with resampled fishing patterns and stochastic parametric recruitment. For the four stocks marked with an asterisk, observed recruitment was used. Stocks areas: Georges Bank (GB), Gulf of Maine (GOM), Cape Cod (CC), and southern New England (SNE).

will be below 50 percent or even below 25 percent of the target at the end of the period modeled (Table 3). That likelihood, although not eliminated, is considerably reduced with the policy that maintains fishing mortality below targets for all of the stocks all of the time (scenario 2). Mean SSB also exceeds the targets for all stocks under scenario 2, whereas it is below targets for 8 of 10 stocks under scenario 1.

Discussion

An unambiguous result from this analysis is that very substantial reductions in fishing effort in the 1980s and early 1990s would have significantly increased the value of the fishery even if the resulting increase in SSB had not led to increased recruitment. With a 60% reduction in nominal effort starting in 1982, annual revenues would have been below those actually realized for only the first 3 years and would have remained well above the observed revenues thereafter.

The total days at sea for groundfish trips ranged from 82 000 to 97 000 during the 1982 to 1993 period and averaged around 93 000. A 60% reduction from a baseline of 93 000 days suggests that the present value of the revenue stream would have been maximized with effort around 37 000 days. It is estimated that over 60 000 days were actually fished in 2001 and another 90 000 were allocated but not used. Thus, even with elimination of the latent effort associated with the unused days, this study suggests that further effort reductions might be required to maximize revenue for the complex.

Like a yield-per-recruit curve, the present value revenue curve for different levels of nominal effort (scenario 1) is relatively flat in the vicinity of the maximum so that a reduction in nominal effort results in a proportionately smaller reduction in value in the vicinity of maximum value. Because cost would be expected to fall along with nominal effort, maximum present value of net operating revenues (PVNR) would likely be achieved with effort well below that which maximizes the present value of gross revenues. Because of the lack of cost data, the effort that would maximize the PVNR was not explicitly modeled; however, an objective of maximizing PVNR would clearly dictate a more conservative strategy than that which maximizes PVR.

The magnitude of the cost reduction that would result from such a large effort reduction coincident with substantial increase in catch rates is uncertain and would depend on a variety of factors. As a result of savings in fixed costs, effort reduction in the form of a reduction in fleet size would have resulted in a substantially greater reduction in costs compared with reductions in fishing by all vessels. However, even a cut in nominal effort implemented with a fleet size reduction would probably not yield a proportional reduction in cost because some costs (including crew) would be affected by the increased volume of fish handled per day fished. Nevertheless, it is instructive to consider the potential magnitude of such a cost reduction relative to the increase in revenues gained with the effort reduction. A vessel cost simulator developed by Lallemand and Gates (1998) suggests that a 12-year-old trawler, 75 feet long, 120 gross tons, with 600 horsepower, based in New Bedford and fishing 200 days of the year in 1993 would have incurred costs (including fixed costs and the opportunity costs of labor for crew and captain) equal to over 90% of its gross revenues. If this ratio held true for the fleet as a whole, a 60% cut in effort might result in cost savings up to six times the magnitude of revenue gains.

A primary objective of this analysis was to compare alternative control rules on fishing effort. The differences in results under alternative control rules are moderate relative to those resulting from effort reduction, but they are instructive nevertheless. In single-species fisheries, maintaining a relatively precautionary fishing mortality such as $F_{0.1}$ generally results in relatively modest reductions in annual harvests and may actually increase net profits relative to F_{MSY} because harvest costs are reduced. However, maintaining precautionary or threshold fishing effort for individual stocks in a multispecies fishery may lead to significant reductions in overall revenues and increase variability of revenues if it is not possible to tune catches of individual stocks. Attempting to maintain SSB in the vicinity of SSB_{MSY} for each individ-

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ual stock is even more problematic because of large fluctuations in recruitment that may be largely independent of fishing pressure.

This retrospective analysis of the northeast multispecies groundfish fishery demonstrates the dilemma managers must face in balancing biological risks and economic concerns. Strict application of current control rules on individual stocks might have significantly lowered total revenue for the overall complex during the period studied and would have increased its annual variation. If, however, higher SSB resulted in higher recruitment, losses from overconstraining fishing on some stocks might have been offset by a reduction in biological risk. A policy maintaining fishing mortality below targets for all stocks in all years might have reduced the probability of SSB falling below critical levels.

In conclusion, the northeast multispecies groundfish fishery has been rebuilding from a depleted state for the last several years (NDSDWG 2001). Nominal effort and fishing mortality have been reduced significantly, but fishing mortality is still above targets for some stocks (NEFMC 2002). Unless better ways can be found to shift effort from weaker to stronger stocks, strict application of control rules regarding overfishing and biomass thresholds will likely continue to require reductions in effort beyond that which maximizes revenues and perhaps profits. This is exemplified by the biological advice provided by Northeast Fishery Science Center staff in June 2002. This advice calculates the reductions in fishing mortality from 2001 necessary to rebuild stocks and eliminate overfishing. Substantial reductions are required for some stocks (e.g., reductions of 94% for Cape Cod yellowtail flounder, 78% for Gulf of Maine cod, and 65% for Georges Bank cod), but mortality on several important stocks could be increased (e.g., increases of 11% for Georges Bank haddock and 16% for Georges Bank yellowtail flounder) (J. Brodziak, Northeast Fisheries Science Center, Woods Hole, MA 02543, personal communication). It may not be possible, and perhaps not desirable, to try to tune fishing mortality on every stock. Furthermore, it may not be possible to achieve biomass targets for all stocks simultaneously because of biological interactions between stocks or cohorts (e.g., predator–prey relationships or cannibalism).

The tools currently used to tune relative catches across stocks (i.e., closed areas and trip limits) are ineffective and inefficient. Trip limits tend to increase regulatory discards. Closed areas, which in their present form were designed primarily to reduce fishing mortality rather than protect habitat or juvenile populations, have increased the cost of taking a given total catch (Holland 2000). It is debatable whether stock-specific total quotas would improve the situation because individual fishers would not have incentives to shift targeting behavior until they were exceeded. Given likely assessment errors, specific total quotas may in fact cause unnecessary biological (quotas set higher than the resource can sustain) and economic (quotas set unnecessarily low) harms. Individual quotas (IQs) might provide the appropriate incentives to shift effort to less heavily fished stocks, but IQ programs are currently unpopular with the fishing industry in the northeast. Even with proper economic and regulatory incentives, the feasibility of tuning relative catches across stocks is unclear because of the spatial overlap and comingling of stocks. It is unrealistic to expect to maintain biomass at or above targets for all stocks at all times without significant reductions in revenues. It may be more appropriate to design control rules and harvest strategies for the overall groundfish complex.

In this study, we considered only technical interactions between the stocks that result from joint harvesting. It is also quite possible that there are biological interactions stemming from predator–prey relationships or resource constraints. Although resource constraints might suggest that benefits from more conservative harvest strategies that keep SSB higher may be less productive than these results suggest, biological interactions can be complex and their effects quite difficult to deduce a priori. However, if they are significant, it may be necessary to broaden the scope of harvest control rules to account for the larger system of biologically interdependent fisheries, and dynamic control rules may be advisable (Collie and Gislason 2001).

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Appendix A

Price models are estimated for each species and market category using data on landings and value of landings from the Northeast Fishery Science Center's commercial fisheries data for the years 1978 through 2000 (this is confidential data, but the aggregate price and quantity data are available from the authors upon request). Price models for four market categories of cod and two market categories of haddock are estimated as a system using a seemingly unrelated linear regression (SUR). Price models for four flatfish species are estimated as a separate (SUR) system. The flatfish system includes price equations for two market categories of yellowtail flounder, witch flounder, and plaice and three categories of winter flounder (the largest of which is referred to as lemon sole). The specifications used for the individual equations were log-linear (i.e., price per kilogram is regressed against the natural logs of the regressors). This allows for a nonlinear demand curve without imposing constant elasticity. Value data is adjusted to year 2000 values using the U.S. gross domestic product (GDP) deflator, and consequently, predicted prices are in 2000 dollars. In most cases, the natural log of real personal disposable income (RPDI) was used in place of an intercept. This effectively creates an intercept that shifts up over time, capturing the positive time trend in real prices for most of the species. Landing quantities are in metric tons live weight. In some cases, the "own" quantity variable with the highest predictive power is aggregate species landings, whereas in other cases it is landings for that market category. For cod, most market category prices are best predicted by landings of market-size cod. Despite parsimonious specifications with only two or three regressors, the price equations are highly significant with R^2 ranging from 0.72 to 0.95. All regressors in all equations are significant at the 0.05 level and most at the 0.01 level. First-order autocorrelation was present and corrected for in both systems of equations. The estimated equations used to predict prices in the simulations and summary statistics for them are given in the equations below. For each year of the simulation, the model calculates the aggregate catch quantities by species and market category according the stock- and species-specific market categorization in Table A1. These quantities are used in the price equations listed below to generate prices by species and market category for that year. The predicted prices are then multiplied by the associated catch quantities to calculate annual revenues.

Table A1. Cohort groupings for different market categories of groundfish and flatfish.

Species	Stock	Market category	Ages included
Cod	GB	Whale	10–15
Cod	GOM	Whale	11–15
Cod	GB	Large	6–9
Cod	GOM	Large	6–10
Cod	GB and GOM	Market	3–5
Cod	GB and GOM	Scrod	1–2
Haddock	GB	Large	3–15
Haddock	GB	Scrod	1–2
Winter flounder	GB	Lemon sole	10–15
Winter flounder	SNE	Lemon sole	7–15
Winter flounder	GB	Large	3–9
Winter flounder	SNE	Large	3–6
Winter flounder	GB and SNE	Small	2
Witch flounder	GB and GOM	Large	9–15
Witch flounder	GB and GOM	Small	5–8
Yellowtail flounder	GB, SNE, and CC	Large	4–15
Yellowtail flounder	GB, SNE, and CC	Small	2–3
American plaice	GB and GOM	Large	7–15
American plaice	GB and GOM	Small	4–6

Note: Correspondence of age classes with market categories can vary by stock area. Stock areas: Georges Bank (GB), Gulf of Maine (GOM), Cape Cod (CC), and southern New England (SNE).

System of equations for groundfish (A1–A6)

$$P_{\text{whalecod},t} = 0.654\ \ln(\text{RPDI}_t) - 0.316\ \ln(Q_{\text{marketcod},t}) - 0.215\ \ln(Q_{\text{largehaddock},t}) \quad R^2 = 0.77 \quad \text{(A1)}$$

$$P_{\text{largecod},t} = 0.905\ \ln(\text{RPDI}_t) - 0.643\ \ln(Q_{\text{marketcod},t}) - 0.114\ \ln(Q_{\text{largehaddock},t}) \quad R^2 = 0.89 \quad \text{(A2)}$$

$$P_{\text{marketcod},t} = 0.803\ \ln(\text{RPDI}_t) - 0.543\ \ln(Q_{\text{marketcod},t}) - 0.106\ \ln(Q_{\text{largehaddock},t}) \quad R^2 = 0.86 \quad \text{(A3)}$$

$$P_{\text{scrodcod},t} = 0.772\ \ln(\text{RPDI}_t) - 0.534\ \ln(Q_{\text{marketcod},t}) - 0.100\ \ln(Q_{\text{largehaddock},t}) \quad R^2 = 0.87 \quad \text{(A4)}$$

$$P_{\text{largehaddock},t} = 0.613\ \ln(\text{RPDI}_t) - 0.383\ \ln(Q_{\text{largehaddock},t}) \quad R^2 = 0.84 \quad \text{(A5)}$$

$$P_{\text{scrodhaddock},t} = 0.532\ \ln(\text{RPDI}_t) - 0.386\ \ln(Q_{\text{scrodhaddock},t}) \quad R^2 = 0.84 \quad \text{(A6)}$$

System of equations for flatfish (A7–A15)

$$P_{\text{lemonsole},t} = 1.341\ \ln(\text{RPDI}_t) - 0.1.197\ \ln(Q_{\text{allwinter},t}) \quad R^2 = 0.84 \quad \text{(A7)}$$

$$P_{\text{largewinter},t} = 1.468\ \ln(\text{RPDI}_t) - 0.867\ \ln(Q_{\text{allwinter},t}) - 0.437\ \ln(Q_{\text{otherflounder},t}) \quad R^2 = 0.87 \quad \text{(A8)}$$

$$P_{\text{smallwinter},t} = 1.538\ \ln(\text{RPDI}_t) - 0.752\ \ln(Q_{\text{allwinter},t}) - 0.657\ \ln(Q_{\text{otherflounder},t}) \quad R^2 = 0.90 \quad \text{(A9)}$$

$$P_{\text{largewitch},t} = 2.723\ \ln(\text{RPDI}_t) - 1.133\ \ln(Q_{\text{largewitch},t}) - 1.400\ \ln(Q_{\text{otherflounder},t}) \quad R^2 = 0.95 \quad \text{(A10)}$$

$$P_{\text{smallwitch},t} = 1.674\ \ln(\text{RPDI}_t) - 1.005\ \ln(Q_{\text{allwitch},t}) - 0.640\ \ln(Q_{\text{otherflounder},t}) \quad R^2 = 0.87 \quad \text{(A11)}$$

$$P_{\text{largeyellowtail},t} = 9.184 - 0.694\ \ln(Q_{\text{allyellowtail},t}) \quad R^2 = 0.72 \quad \text{(A12)}$$

$$P_{\text{smallyellowtail},t} = 8.650 - 0.704\ \ln(Q_{\text{allyellowtail},t}) \quad R^2 = 0.81 \quad \text{(A13)}$$

$$P_{\text{largeplaice},t} = 15.321 - 0.903\ \ln(Q_{\text{allplaice},t}) - 0.476\ \ln(Q_{\text{otherflounder},t}) \quad R^2 = 0.93 \quad \text{(A14)}$$

$$P_{\text{smallplaice},t} = 14.378 - 0.179\ \ln(Q_{\text{allplaice},t}) - 1.110\ \ln(Q_{\text{otherflounder},t}) \quad R^2 = 0.93 \quad \text{(A15)}$$

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The importance of habitat quality for marine reserve – fishery linkages

Lynda D. Rodwell, Edward B. Barbier, Callum M. Roberts, and Tim R. McClanahan

Abstract: We model marine reserve – fishery linkages to evaluate the potential contribution of habitat-quality improvements inside a marine reserve to fish productivity and fishery catches. Data from Mombasa Marine National Park, Kenya, and the adjacent fishery are used. Marine reserves increase total fish biomass directly by providing refuge from exploitation and indirectly by improving fish habitat in the reserve. As natural mortality of the fish stock decreases in response to habitat enhancement in the reserve, catches increase by up to 2.6 tonnes (t)·km^{-2}·year^{-1} and total fish biomass by up to 36 t·km^{-2}. However, if habitat-quality improvement reduces the propensity of fish to move out of the reserve, catches may fall by up to 0.9 t·km^{-2}·year^{-1}. Our results indicate that habitat protection in reserves can underpin fish productivity and, depending on its effects on fish movements, augment catches.

Résumé : La modélisation des liens entre une réserve marine et une pêche commerciale nous a permis d'évaluer la contribution potentielle de l'amélioration de la qualité de l'habitat dans la réserve à la productivité des poissons et à la récolte. Des données provenant du parc national marin de Mombasa, au Kenya, et des pêches commerciales de la région ont servi a démontrer que les réserves marines accroissent la biomasse totale des poissons directement, en procurant des refuges contre l'exploitation, et indirectement, en améliorant la qualité de l'habitat dans la réserve. À mesure que la mortalité naturelle du stock de poissons diminue à la suite de l'amélioration de l'habitat dans la réserve, l'augmentation des prises peut atteindre 2,6 tonnes (t)·km^{-2}·an^{-1} et celle de la biomasse totale des poissons 36 t·km^{-2}·an^{-1}. Cependant, si l'amélioration de la qualité de l'habitat réduit la tendance des poissons à quitter la réserve, la réduction des prises peut atteindre 0,9 t·km^{-2}·an^{-1}. Nos résultats indiquent que la protection de l'habitat dans les réserves peut soutenir la productivité des poissons et, selon son effet sur les déplacements, augmenter les prises.

[Traduit par la Rédaction]

Introduction

The deterioration of marine habitats and the depletion of fish stocks worldwide are of major concern to fisheries managers and conservationists (Agardy 2000). It is believed that habitat loss is the single greatest cause of the worldwide decline in biodiversity (Wilcove et al. 1998) and has serious implications for ecosystem functioning and integrity (Walters and Wethey 1996). Some of the most threatened habitats include coastal estuarine habitat (such as mangroves) and coral reefs.

Fishing with destructive fishing gears is a major cause of habitat deterioration in many temperate and tropical regions. Seabed habitat has been greatly degraded and even destroyed by the direct effects of dredging, trawling, long-lining, and dynamite fishing (Dayton et al. 1995; Roberts 1995). Despite this, it is only recently that research has focused on the effects of fishing on habitat structure and the potential implications for associated faunal communities (Jennings and Kaiser 1998; Turner et al. 1999). Though some ecologists have worked on the relationship between benthic community ecology and fish habitat function (e.g., Dayton et al. 1995), less research has focused on the implications of damage to habitat for demersal fishes. Habitat is known to profoundly affect the productivity of a fish stock and is therefore believed to be fundamentally important to fishery production (Dayton et al. 1995). For example, studies on the impact of loss of mangroves, often the result of deforestation and aquaculture expansion (Spalding et al. 1997), indicate that the losses to the fishery may be considerable because mangrove forests act as nursery grounds for the fishery (Barbier 2000). However, the direct impact of the degradation of coral reef habitat on fisheries is as yet uncertain.

Fisheries management tools such as taxes, quotas, and licenses fail to protect essential habitats such as coral reefs because habitat loss or degradation can occur at even low levels of fishing effort (National Research Council 2000). Many researchers have pointed out the necessity of habitat protection for sustainable marine resource exploitation (e.g., Roberts 1997*b*; Benaka 1999). In response, marine-protected areas have increasingly been established to tackle the prob-

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lems of biodiversity loss and habitat deterioration and more recently have gained support as a fisheries management tool that can help to enhance fish stocks (Lauck et al. 1998; Conover et al. 2000; Roberts et al. 2001). Reserves appear to be the best management tool for the restoration and preservation of the structure and functioning of entire ecosystems on which fisheries depend (Conover et al. 2000). They can also ease problems of by-catch, which can perturb ecosystems at local and regional levels (Collins et al. 2000). Areas protected from fishing invariably support higher levels of fish biomass and diversity (for review, see Halpern (2003)). However, although new results indicate that the reserve concept is sound (Roberts et al. 2001), the fishery benefits of reserve establishment are still being debated and the contribution of habitat protection to catches has yet to be fully determined.

Despite wide recognition that marine reserves allow the recovery of degraded marine habitat (e.g., Koenig et al. 2000; Roberts 2000*a*), models of marine reserves fail to consider explicitly the contribution of habitat quality to the fishery (e.g., Holland and Brazee 1996; Hannesson 1998; Sanchirico and Wilen 2001). In this paper we add to these studies by investigating the ecosystem value of marine reserves, evaluating the specific contribution of habitat-quality improvements inside a marine reserve to fish productivity and fishery catch in adjacent fishing grounds. We focus on a tropical marine reserve that protects a coral reef habitat. We extend the model in Rodwell et al. (2002), which focused on the processes of fish and larval movement patterns between reserve and fishing ground, optimal reserve size, and exploitation rates, by including an explicit habitat-quality term — a live coral cover proxy. Rugosity (a measure of the roughness of the substrate) could also be used as a habitat-quality proxy. In a model investigating the effects of seafloor habitat on juvenile cod survivorship, Lindholm et al. (2001) use vertical relief as a measure of habitat complexity. Rodwell et al. (2002) found that under almost all movement conditions (not a closed system), a reserve could enhance catches in a moderately to heavily exploited fishery (≥40% exploitation rate). They assume spatial homogeneity in the marine management area, acknowledging that this as an oversimplification. In this study, we consider two processes that may be affected by habitat-quality improvements in the marine reserve. The first is the decrease in natural mortality of the fish stock in response to habitat enhancement in the reserve. This positive relationship between habitat complexity and survivorship of coral reef fishes has been supported by many field studies (e.g., Roberts and Ormond 1987; McClanahan 1994). The second process considered is the restriction of movement of fish from the reserve to the fishing grounds as habitat quality improves inside the reserve. We consider habitat selection (discussed by MacColl (1990)) in two ways: (*i*) initially we assume the simplified case of fish moving in a density-dependent fashion irrespective of habitat quality, and (*ii*) then we consider a behavioural response of fish to the habitat-quality gradient between reserve and fishing grounds by restricting movement. This is similar to the movement patterns described by MacCall (1990) in which immigration and emigration are affected by gradients in quality of local habitat.

We use Mombasa Marine National Park (MNP) and adjacent fishing grounds as the case study site. Both live coral cover and fish biomass have increased significantly inside Mombasa MNP since its establishment (McClanahan and Kaunda-Arara 1996; Rodwell 2001). Though the exact relationship between fish biomass and habitat quality is uncertain, improved habitat quality could provide more food and refuge for fish, thereby reducing natural mortality levels (Dayton et al. 1995; Walters and Wethey 1996). This effect of habitat quality on natural mortality alone we term the "single habitat-quality effect". We test three relationships between natural mortality and habitat quality: logarithmic, linear, and polynomial.

The habitat-quality effect on the movement of fish is difficult to determine in the field and is likely to vary among species. We consider a "double habitat-quality effect" in which both the natural mortality of the fish stock declines in response to habitat-quality improvements and the habitat-quality gradient between the reserve and fishing grounds slows the rate of fish movement out of the reserve. This could have negative implications for fishery catches if the spillover from reserves to fishing grounds is significantly reduced.

In the following section we describe the model of marine reserve – fishery linkages. We then apply the model to a case study, Mombasa MNP and its adjacent fishery. We carry out sensitivity analysis to determine the implications of various habitat quality effects on the fishery in terms of catch, total fish biomass, and the exploitation rate at which it becomes profitable to establish a reserve. Results indicate that habitat-quality improvements are likely to make a significant contribution to the fishery.

The model

This deterministic and discrete-time model describes the dynamics of a fish stock subdivided between a fully protected marine reserve and adjacent fishing grounds. The term fully protected refers to protection from fishing only. Tourist activities such as diving and snorkelling can still take place inside the reserve. The total stock comprises two distinct substocks, X_1 and X_2 that occupy the reserve and the fishing grounds, respectively. The reserve habitat quality (q_1) is dependent on time since reserve establishment (t), i.e., $q_1 = q(t)$. The habitat quality of the fishing grounds is represented by q_2. In reality, q_2 is likely to decline over time if exploitation continues. In this model we take a constant base level of habitat quality in the fishing grounds to give a conservative estimate of the habitat-quality gradient between reserve and fishing grounds. As the reserve is fully protected from fishing, there is only catch (H) from the fishing grounds. The dynamics between the reserve and the fishing grounds are described by the transfer of recruits resulting from larval dispersal (T) and the movement of fish (M). Both fish and larval movement are explicitly modelled by employing a spawner–recruit relationship. The difference equation system describing the dynamics of the reserve and fishing ground stocks is given by eqs. 1 and 2:

$$(1)\quad X_{1,t+1} = (1 - \mu_1(q_{1,t}))X_{1,t} + R(X_{1,t}) - M(\bar{X}_{1,t}, \bar{X}_{2,t}, \alpha, \sigma, q_{1,t}, q_2) - T(R_{1,t}, R_{2,t}, \alpha, \theta)$$

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$$X_{2,t+1} = (1 - \mu_2)X_{2,t} - H(X_{2,t}) + R(X_{2,t}) + M(\overline{X}_{1,t}, \overline{X}_{2,t}, \alpha, \sigma, q_{1,t}, q_2) + T(R_{1,t}, R_{2,t}, \alpha, \theta) \quad (2)$$

$X_{1,t}$ denotes the biomass of the fish stock in the reserve at time t, and $X_{2,t}$ represents the biomass of the fish stock in the fishing grounds at time t. In this study we do not consider a particular species but an aggregated fish stock because of the lack of complete species-specific catch data. $\mu_1(q_{1,t})$ and μ_2 are the average natural mortality estimates measured as a proportion of fish biomass levels X_1 and X_2, respectively. The natural mortality of the fish stock in the reserve varies with the level of habitat quality, i.e., $\mu_{1,t} = \mu(q_{1,t})$. $q_i = C_i/A_i$ for $i = 1, 2$, where C_i is the area of live coral cover of i (in km^2) and A_i is the area of i (in km^2). $M(\overline{X}_{1,t}, \overline{X}_{2,t}, \alpha, \sigma, q_{1,t}, q_2)$ is the net movement of fish between the reserve (area 1) and the fishing grounds (area 2) in time period t, where the density of stock i is given by $\overline{X}_{i,t} = X_{i,t}/A_i$, $i = 1, 2$. α is the proportion of management area protected, i.e., $\alpha = A_1/A$, where A represents the total management area. σ is the mobility coefficient of fish. The net fish movement can be positive or negative depending on the comparative stock densities. If the stock density within the reserve is greater than the stock density in the fishing grounds, the net fish movement is positive (i.e., outward from the reserve to the fishing grounds) and vice versa. Similarly, the transfer of recruits resulting from larval dispersal, $T(R_{1,t}, R_{2,t}, \alpha, \theta)$ can be positive or negative. $R(X_{1,t})$ and $R(X_{2,t})$ represent recruit production for stocks X_1 and X_2, respectively at time t. θ is the proportion of larvae retained. The remaining larvae disperse. Catch is treated simply as a function of fish biomass in the fishing grounds i.e., $H_t = H(X_{2,t})$.

Functional forms

Habitat quality over time

Habitat quality can be influenced by many factors such as time since protection, pollution, tourist visitation, fishing effort, and effects such as coral bleaching. However, in Mombasa MNP and the adjacent fishing grounds, pollution is not a significant problem (Mwangi et al. 2001). If pollution affects the area at all, we assume that it does so evenly and so does not contribute to a habitat-quality gradient between the reserve and the fishing grounds. Furthermore, damage resulting from tourist activities such as diving and snorkelling is limited (Muthiga and McClanahan 1997). By far the most significant factor in determining habitat quality is the substrate's complexity, which is closely correlated to live coral cover (Rodwell 2001; T.R. McClanahan, unpublished data). Highly complex substrate provides refuge for fish, thereby reducing mortality rates and increasing fish abundance. In Kenya, high catch intensity in fishing grounds has reduced the number of sea urchin predators, allowing the population of sea urchins to burgeon. In turn sea urchins scrape the corals, reducing diversity and complexity (McClanahan 1994). In this paper we focus our analysis on the case in which protection allows habitat quality to gradually improve (i.e., live coral cover to increase) inside the marine reserve.

Reserve habitat quality is treated as a variable dependent on time since protection. The data from Mombasa MNP indicate a positive relationship between live coral cover and time since protection up until the coral bleaching event of March 1998 when live coral cover fell dramatically (McClanahan and Kaunda-Arara 1996; Rodwell 2001; T.R. McClanahan, unpublished data). Episodic impacts such as coral bleaching are beyond the scope of this study; therefore, only data from 1987 to 1997 are used to estimate the "habitat quality over time since protection" function for the model (Fig. 1).

In the fishing grounds adjacent to Mombasa MNP, habitat quality has remained fairly constant since reserve establishment. However, inside the reserve, habitat quality has increased significantly over time. The habitat-quality differential ($\bar{q}_t$) between Mombasa MNP and the unprotected fishing grounds increased between 1987 ($t = 1$) and 1997. The best "realistic" fit for $\bar{q}_t$ is the logarithmic function given by eq. 3. Although power, cubic, and quadratic functions fit the data better over the 10 years of data, when extrapolated over the 30 years, they gave unrealistic ranges.

$$\bar{q}_t = q_{1,t} - q_{2,t} = a_1 \ln t + a_2 \quad (3)$$

where $a_1 = 14.8$ and $a_2 = 0.67$. This gave an R^2 estimate of 0.79 and $p = 0.003$. Despite this high R^2, this function may not accurately portray the trend in $\bar{q}_t$ over time. It is likely that $\bar{q}_t$ will level off rather than continue to increase. By using this function in the model simulations, the habitat-quality effect on natural mortality may be overstated. However, the relationship was extrapolated over 30 years for the simulations and the range of $\bar{q}_t$ was $0\% \leq \bar{q}_t \leq 51\%$ from time $t = 1$ to $t = 30$, respectively. This seems highly plausible because the differential observed in the field reached approximately 40% after less than 10 years (Rodwell 2001).

The habitat-quality gradient between the reserve and fishing grounds tends to a factor of 5 ($q_1/q_2 \approx 0.55/0.11$) and so the inverse gradient, which influences the rate of fish movement, tends to 0.2 ($q_2/q_1 \approx 0.11/0.55$). The greater the difference in habitat quality of the two areas, the greater the effect on fish movement.

Natural mortality vs. habitat quality

Natural mortality of fish inside the reserve is a variable dependent on reserve habitat quality, i.e., $\mu_1(q_{1,t})$. The empirical data from Mombasa could not confirm the exact relationship between habitat quality and fish biomass or natural mortality rates, though fish biomass was positively associated with live coral cover (Rodwell 2001). Three functions are explored in the model simulations to simply illustrate possible contrasting changes in natural mortality resulting from habitat-quality improvements (Fig. 2). In each case, natural mortality is assumed to be negatively related to habitat quality, i.e., $\mu'(q_1) < 0$. In the polynomial function, mortality falls at an increasing rate, $\mu''(q_1) > 0$. In the linear function, it falls at a constant rate, $\mu''(q_1) = 0$. In the logarithmic function, it falls at a decreasing rate, $\mu''(q_1) < 0$. The natural mortality rate in each case is assumed to stabilise after 30 years. This time acts as a threshold beyond which natural mortality does not fall any further. Rodwell (2001) found an exponential relationship between fish biomass and the "reserve effect" (i.e., the presence of the reserve). This implies that the logarithmic function may be the most appropriate fit for the fish biomass and natural mortality relationship (assuming an inverse relationship exists between fish

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Fig. 1. Habitat-quality (live coral cover) differential between Mombasa Marine National Park and the adjacent fishing grounds ($q_1 - q_2$) versus time since reserve establishment.

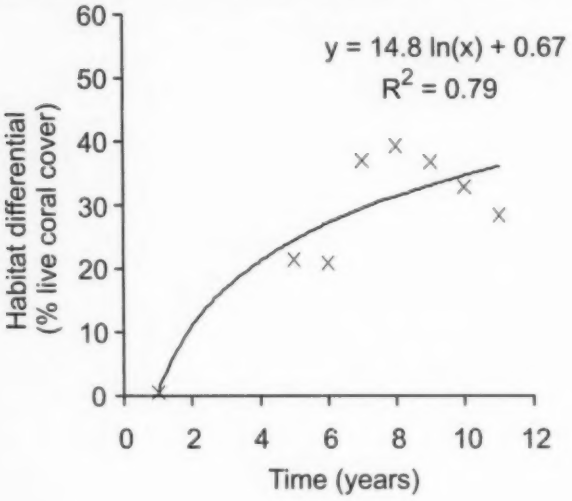
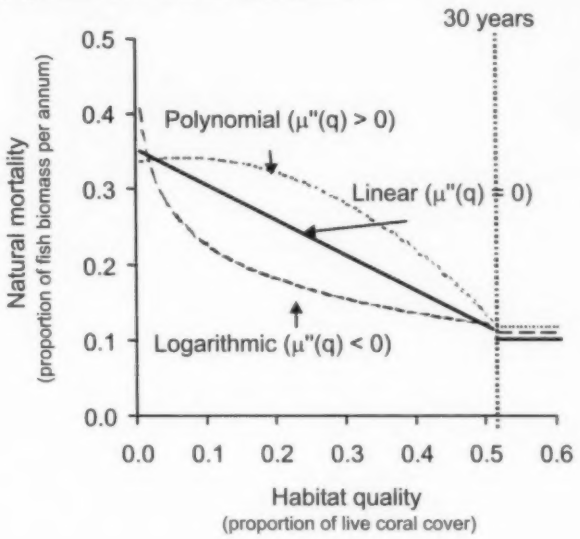


Fig. 2. Three relationships modelled between natural mortality of fish and habitat quality in the reserve: logarithmic, linear, and polynomial (over 30 years of protection).



biomass and natural mortality and the reserve effect includes habitat-quality improvement). We use realistic ranges of natural mortality based on the literature (Pauly and Ingles 1981; between 10 and 40% per annum) and fit the functions within these ranges. A proportion of the fivefold increase in fish biomass density resulting from reserve creation could be accounted for by the increase in the natural survival rate from 60 to 90%. The details of the functions are given below.

Polynomial function: $\mu(q_1) = -d_1(q_1)^2 + d_2q_1 + d_3$, where $d_1 = 1.12$, $d_2 = 0.16$, and $d_3 = 0.34$. For this relationship, the range of μ_1 was $0.13 \leq \mu(q_1) \leq 0.34$ for 30 years and μ_2 remained constant at 0.34. Beyond 30 years, $\mu_1 = 0.13$.

Linear function: $\mu(q_1) = -c_1q_1 + c_2$, where $c_1 = 0.47$ and $c_2 = 0.35$. In this case, the range of μ_1 was $0.11 \leq \mu(q_1) \leq 0.35$ for 30 years and μ_2 remained constant at 0.35. Beyond 30 years, $\mu_1 = 0.11$.

Logarithmic function: $\mu(q_1) = -b_1\ln q_1 + b_2$, where $b_1 = 0.066$ and $b_2 = 0.076$ and the range of μ_1 was $0.12 \leq \mu(q_1) \leq 0.4$ for 30 years and μ_2 remained constant at 0.4. Beyond 30 years, $\mu_1 = 0.12$.

With these levels of natural mortality (0.4, 0.35, 0.34) in the fishing grounds, the exploitation range tested was $0.1 \leq \omega \leq 0.6$.

The simulations were run for 30 years. Beyond the 30-year time period, the natural mortality of the reserve is assumed to stabilise. The functional forms used are to simply illustrate different response rates over the 30-year time period only.

Fish movement

The movement of fish is a function of the habitat-quality gradient between the reserve and the fishing grounds. We include the (inverse) habitat-quality gradient in the movement function, i.e., $M_t = f(q_2/q_{1,t}, \rho)$, where ρ represents the degree to which the habitat-quality gradient slows down the movement process. A potential impact of habitat-quality improvements is that the protected region will provide more food and refuge. This can result in a lower proportion of fish biomass leaving the reserve, which may counter the density-dependent movement effect. In their study, Lindholm et al. (2001) assume that the movement rate of juvenile cod from an area is the inverse of the habitat complexity score for that area. The fish movement function used in this model is given by

$$(4) \qquad M_t = \sigma A\alpha(1-\alpha)\left[\left(\frac{q_2}{q_{1,t}}\right)^{\rho}\overline{X}_{1,t} - \overline{X}_{2,t}\right]$$

where $0 \leq \sigma \leq 1$, $0 \leq \rho \leq 1$, $dM_t/d\rho < 0$ (i.e., as ρ increases, fish movement out of the reserve declines) and $dM_t/d(q_{1,t}/q_2) < 0$ (i.e., as the habitat quality inside the reserve improves, relative to fishing ground habitat quality, fish movement out of the reserve declines). Therefore, $dM_t/d(q_2/q_{1,t}) > 0$. By substituting $\overline{X}_1 = X_1/\alpha A$ and $\overline{X}_2 = X_2/(1-\alpha)A$ and cancelling through, eq. 4 can also be written as

$$M_t = \sigma[(q_2/q_{1,t})^{\rho}(1-\alpha)X_{1,t} - \alpha X_{2,t}]$$

If $\rho = 0$, there is no habitat effect on fish movement. We refer to this as the single habitat-quality effect, i.e., habitat quality only affects natural mortality. If $0 < \rho \leq 1$, then the habitat-quality gradient slows down the movement of fish from the reserve to the fishing grounds, which we term the double habitat-quality effect because both natural mortality and fish movement are affected by habitat-quality changes. If $\rho = 1$, the restriction to movement could be strong depending on the magnitude of the habitat-quality gradient between the reserve and fishing grounds. σ represents the natural mobility coefficient of the fish stock, which is influenced by life history characteristics rather than by environmental factors.

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Other functional forms

Other functional forms are the same as those used in Rodwell et al. (2002), which are summarised below.

Catch (H)

In this model, we take catch levels to be privately determined in the fishery reflecting the property rights in place. The catch function used is a simple linear relation between catch and biomass in the fishing grounds:

$$(5) \qquad H_t = \omega X_{2,t}$$

where ω is a constant representing the exogenous exploitation rate as proportion of the exploitable fish biomass $X_{2,t}$; ω may reflect the rate at which marginal benefits equate with marginal costs (optimal fishing policy in remaining fishing grounds) or total revenues equate with total costs (open access in remaining fishing grounds). This type of catch function may also represent a linear total allowable catch quota system (such as that used by Conrad 1999).

Recruit production (R_1 *and* R_2)

A proportion of biomass X is taken as a proxy for spawning stock biomass and so the Beverton–Holt recruit production function for the reserve is

$$(6) \qquad R_{1,t} = \varepsilon_1 X_{1,t}/(\gamma_1 \varepsilon_1 X_{1,t} + \beta_1)$$

where $R_{1,t}$ is the recruit production of the reserve fish stock in time period t; $X_{1,t}$ is the reserve fish biomass in time period t; γ_1 and β_1 are recruitment parameter estimates for the reserve stock for a given initial growth rate; and ε_1 is the proportion of the reserve fish biomass that is reproductively mature.

For the fishing ground stock, the Beverton–Holt recruit production function is

$$(7) \qquad R_{2,t} = \varepsilon_2(X_{2,t} - H_t)/[\gamma_2 \varepsilon_2 (X_{2,t} - H_t) + \beta_2]$$

where ε_2 is the proportion of the fishing ground stock that is reproductively mature. We make two assumptions about recruit production in the fishing grounds. (*i*) ε_1 and ε_2 are constant over the time period. We take the mean values of ε_1 and ε_2 over the time period from the Mombasa data. Alternatively, ε_1 and ε_2 would vary over time. (*ii*) The only spawners are those remaining after catch, i.e., $\varepsilon_2(X_2 - H)$ in each time period (for discussion, see Rodwell et al. (2002)).

Recruit transfer (T)

Larval movement patterns are described by the larval retention factor θ. The recruit transfer function is

$$(8) \qquad T_t = (1 - \theta)[(1 - \alpha)R_{1,t} - \alpha R_{2,t}] \quad \text{for } 0 \le \theta \le 1$$

where θ is the proportion of larvae retained. This will depend on the relationship between dispersal distance, the reserve size (and shape) (Carr and Reed 1993), currents (Roberts 1997*a*), tides, and the swimming capabilities of the larvae (Warner et al. 2000). If $\theta = 0$, then there is no larval retention and the larvae disperse uniformly. If $\theta = 1$, then full retention of larvae occurs. This results in no transfer of recruits between the reserve and the fishing ground.

Steady-state equations

The steady-state equations for the reserve and fishing ground stocks are given by eqs. 9 and 10, respectively:

$$(9) \qquad -\mu_1(q_1^*)X_1^* - \sigma A\alpha(1-\alpha)\left[\left(\frac{q_2}{q_1^*}\right)^{\theta}\overline{X}_1^* - \overline{X}_2^*\right] + \alpha(1-\theta)\left[\frac{\varepsilon_1 X_1^*}{\gamma_1\varepsilon_1 X_1^* + \beta_1} + \frac{\varepsilon_2(1-\omega)X_2^*}{\gamma_2\varepsilon_2(1-\omega)X_2^* + \beta_2}\right] + \theta\left[\frac{\varepsilon_1 X_1^*}{\gamma_1\varepsilon_1 X_1^* + \beta_1}\right] = 0$$

$$(10) \qquad -(\mu_2 + \omega)X_2^* + \sigma A\alpha(1-\alpha)\left[\left(\frac{q_2}{q_1^*}\right)^{\theta}\overline{X}_1^* - \overline{X}_2^*\right] + (1-\alpha(1-\theta))\left[\frac{\varepsilon_1 X_1^*}{\gamma_1\varepsilon_1 X_1^* + \beta_1} + \frac{\varepsilon_2(1-\omega)X_2^*}{\gamma_2\varepsilon_2(1-\omega)X_2^* + \beta_2}\right] - \theta\left[\frac{\varepsilon_1 X_1^*}{\gamma_1\varepsilon_1 X_1^* + \beta_1}\right] = 0$$

From these equations we derive X_1^* and X_2^* from which we can determine total biomass ($X_1^* + X_2^*$) and catch ($H^* = \omega X_2^*$). The values of total biomass and catch with habitat-quality effects can then be compared with the values with no habitat-quality effect.

Model application

Before using the model to determine the conditions in which reserve habitat-quality improvements augment fish biomass and catch levels, we first apply the model using data from Mombasa MNP and its adjacent fishery. Mombasa MNP is a marine reserve on the Kenyan coast fully protected from fishing. It was officially established in 1987–1988 but did not achieve full enforcement until 1992 (McClanahan and Kaunda-Arara 1996). The adjacent fishery is one of semisubsistence. Fish biomass and substrate data have been collected using replicate visual transects and line transects at sites inside and outside the reserve since 1987 by T.R. McClanahan and colleagues at the Coral Reef Conservation Project in Mombasa. Catch data have also been collected at fish-landing sites adjacent to the marine reserve since 1991. These catch data are not complete because of various data collection problems such as night fishing and fishers taking home catches, which are therefore not recorded. However, they do provide an indication of catch trends. A full description of data and the study site is given in Rodwell (2001).

The model simulations were run using STELLA®, which is a simultaneous difference equation solver developed by High Performance Systems (www.hps-inc.com).

Parameter estimates

We assume moderate levels of fish movement ($\sigma = 0.2$) equivalent to between 5 and 12% of the reserve stock spilling over into the fishing grounds per annum (Rodwell et al.

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Fig. 3. A comparison of recorded (open circles) and predicted (solid diamonds) catch per unit area for the Mombasa fishery (60% exploitation) for the 12 years after reserve establishment. The official time of reserve establishment is 1988; 1992 is the time of full enforcement.

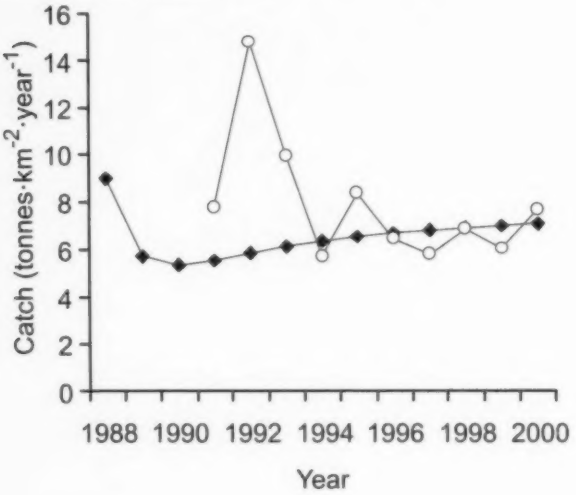
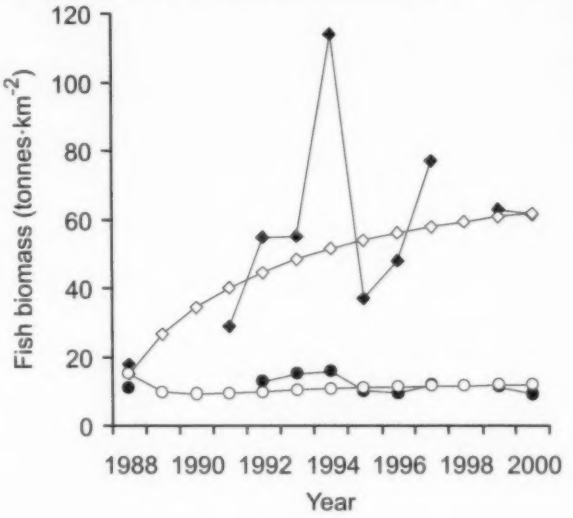


Fig. 4. A comparison of recorded (solid symbols) and predicted (open symbols) fish biomass levels in the reserve (diamonds) and fishing grounds (circles) in the Mombasa fishery (60% exploitation) for the first 12 years after reserve establishment.



2002) and 50% larval retention ($\theta = 0.5$). The initial growth rate of 85% was estimated from data on fish biomass growth in Mombasa MNP (Rodwell 2001). γ_1 and γ_2 were estimated given the values of μ_1 and μ_2. The remaining parameter estimates used in the simulations were as follows: $\mu_1 = 0.1$ to 0.4; $\mu_2 = 0.4$ (logarithmic), 0.35 (linear), and 0.34 (polynomial); $\gamma_1 = 0.00548$ (logarithmic), 0.00575 (linear), and 0.00581 (polynomial); $\gamma_2 = 0.00234$ (logarithmic), 0.00246 (linear), and 0.00248 (polynomial); β_1, $\beta_2 = 0.1$; $\varepsilon_1 = 0.7$; $\varepsilon_2 = 0.2$; $q_{1,t} = 0.11$ to 0.51; $q_2 = 0.11$; $\alpha = 0.3$; $\rho = 0$ to 1; and $\omega = 0$ to 0.6.

Results

The Mombasa case was best represented by the results for 60% exploitation (the highest exploitation rate run with this model). Of the three habitat quality – natural mortality functional forms, the logarithmic form represented the data best, with catches and fish biomass levels stabilising as they appear to be doing in Mombasa MNP and the fishing grounds. For each functional form, the closest catch and biomass levels to the recorded data were achieved for the case when $\rho = 0$, i.e., when there was only a single habitat-quality effect and no effect on fish movement out of the reserve.

Fishery catch

The year of reserve establishment was taken as 1988. However, catch data were only available from 1991 onwards. The catch per unit area in 1992 was very high, 14.8 tonnes (t)·km^{-2}·year^{-1} (Fig. 3), but this may be attributable to poaching in the reserve during that year. The end of 1992 may represent the time of true full enforcement of the park (McClanahan and Kaunda-Arara 1996). This would explain the difference in model results and recorded catch per unit area over the 1988–1994 period (Fig. 3). However, the model predictions towards the end of the 13-year period are very close to the recorded data.

Fish biomass

Fish biomass data were available from 1988 (McClanahan 1994; McClanahan and Kaunda-Arara 1996; T.R. McClanahan, unpublished data). For the years between 1988 and 1991, Mombasa MNP was only partially protected. The model predictions are very close for the fishing grounds case but the reserve case was more variable, fluctuating about the predicted values (Fig. 4). In the sensitivity analysis, we compare the steady-state results (after 30 years).

Sensitivity analysis

In this section, we explore the potential consequences of habitat-quality changes on catches and total fish biomass levels for different scenarios of habitat-quality effects, exploitation rates, and relationships between natural mortality and habitat quality.

Methods

Firstly, we simulated the scenario of a reserve without a habitat-quality effect. We then considered the single habitat-quality effect ($\rho = 0$). The results were compared with the without habitat-quality effect scenario to determine the percent increase or decrease in catch and total biomass levels resulting from habitat-quality effects. We did this for each of the functional forms of natural mortality versus habitat quality (logarithmic, linear, and polynomial).

We tested the double habitat-quality effect in which fish movement is also dependent on habitat quality. The absolute values of q_1 and q_2 are used in this case. This allowed for a meaningful habitat-quality ratio, $q = q_1/q_2$, to be used for the movement function. $q_1 = q_2 = 0.11$ at time $t = 0$. $q_1(t)$ varied

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as a logarithmic function with time, whereas q_2 remained constant at 0.11 (the approximate proportion of live coral cover when the reserve was established in 1987–1988). The sensitivity of results to the value of ρ was tested. We then compared these results with those of the without habitat-quality effect.

To illustrate the potential impact of habitat-quality effects on the optimal combination of reserve size and exploitation rates, we compared the results of catch levels under different scenarios: with no reserve; with a reserve without habitat-quality effect; with a single habitat-quality effect; and with moderate (ρ = 0.5) and strong (ρ = 1) double habitat-quality effects. We used the scenario of logarithmic habitat-quality effect, 85% initial growth rate and 30% reserve size, i.e., α = 0.3 (based on the Mombasa case).

Results

Without habitat-quality effect

The results (given in Table 1) are steady-state levels of catch and total fish biomass (30 years after reserve protection). Highest total fish biomass levels were achieved when exploitation was lowest and vice versa, ranging from 416 t (16 t·km^{-2}) at an exploitation rate of 60% (ω = 0.6) to 1050 t (39 t·km^{-2}) at an exploitation rate of 10% (ω = 0.1) (for the logarithmic function). The total management area is 26.75 km^2. The highest catch levels (when the reserve covers 8 km^2 of the management area, 30%, i.e., α = 0.3) were achieved when the exploitation rate was 40% (ω = 0.4) and the lowest when exploitation was 10% (ω = 0.1), ranging from 68 t·km^{-2} (3.6 t·km^{-2}·year^{-1}) to 126 t·km^{-2} (6.7 t·km^{-2}·year^{-1})(for the logarithmic function). The single and double habitat-quality effects results are compared with these results in the following sections. Note that at the time of reserve establishment (t = 0), the natural mortality levels in the whole management area are equal, i.e., $\mu(t = 0) = \mu_1(t = 0) = \mu_2(t = 0)$.

Single habitat-quality effect

What if natural mortality declines in response to habitat-quality improvements?

The greatest habitat-quality effect for both catch and total biomass was found when exploitation is the highest level (ω = 0.6) and the least effect was noted when exploitation is the lowest level (ω = 0.1) (Table 2). This is consistent with the findings of other studies (e.g., Holland and Brazee 1996; Sladek-Nowlis and Roberts 1997). Catches were found to increase by between 13 and 39% (0.5–2.6 t·km^{-2}·year^{-1}). This range is due to both different exploitation rates and functional relationships between habitat quality and natural mortality. Total fish biomass increased by between 40 and 92% (7–36 t·km^{-2}).

Under our assumptions, improvements in habitat quality always result in increased total fish biomass. The greatest habitat-quality effect in terms of both catch and total fish biomass was with the logarithmic functional relationship between habitat quality and natural mortality. This can be explained by the immediate rapid decline in natural mortality as a result of small improvements in habitat (see Fig. 2). This may vary from species to species according to the degree of dependence on live coral cover and associated benthic complexity.

Double habitat-quality effect

What if natural mortality declines and fish movement is hindered in response to improving habitat quality in the reserve?

The results of the double habitat-quality effects (shown in Table 2) are again with respect to the without habitat-quality effect values. As for the single habitat-quality effect, the greatest effect is when exploitation is most intense (ω = 0.6) and least effect when exploitation is low (ω = 0.1). The results of the moderate double habitat-quality effect (i.e., when ρ = 0.5) indicate small increases in catch between 1 and 15% (0.04–1 t·km^{-2}·year^{-1}) for all functional forms and large increases in biomass between 51 and 130% (9–51 t·km^{-2}) resulting from the habitat-quality effects.

In the case of a strong habitat-quality effect on movement (ρ = 1), habitat quality limits fish movement so much that catches can decline by between 3 and 12% (0.1–0.9 t·km^{-2}·year^{-1}) depending on the functional form and the exploitation rate. However, the total fish biomass level is even higher than the moderate effect between 55 and 156% (9–61 t·km^{-2}) because more fish remain protected inside the reserve. The increase in fish biomass will be seen inside the reserve only because fish will stay inside the reserve, increase in individual size, and produce more eggs. In fact, fish biomass in the fishing grounds will decline because of the low "spillover" rate. This accounts for the fall in catch (by up to 12%).

The catch levels with single and double and without habitat-quality effects are similar whether the fishery is facing low or high exploitation, only the magnitudes differ (see Fig. 5). Catches are highest with the single habitat-quality effect because there is no effect on fish movement. Spillover into the fishing grounds can therefore result in an increase in catches. The lowest catches are seen when the movement effect is strongest (ρ = 1). In this case, the habitat quality gradient effect outweighs the density-dependent effect and the fish stay inside the reserve. Even if this were the case, the fall in catches would be small, between 3 and 12%. We can see that even if ρ = 0.8 (still a high restriction on fish movement), catches can be higher than without a habitat-quality effect (Fig. 5).

Of the possible habitat-quality effects on catch (shown in Fig. 6), the scenario which best illustrated the Mombasa case is that of a single habitat-quality effect. In this case, catches will be greater with the 30% reserve than without when the exploitation rate exceeds 20% of exploitable biomass. This compares to approximately the 30% exploitation rate when there is no habitat-quality effect (Rodwell et al. 2002). The strong double habitat-quality effect would result in a higher level of exploitation at which it becomes preferable to create a reserve (approximately 34%).

The highest total fish biomass levels are reached when there is the highest movement effect, ρ = 1 (see Fig. 7). The lowest total fish biomass levels occur when habitat neither reduces natural habitat nor restricts movement out of the reserve, i.e., the case without a habitat-quality effect.

Discussion

Most economic studies have failed to consider habitat-quality improvement as an economic benefit of marine reserves (but see Mangel (2000)). In this study, we have high-

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Table 1. Range of equilibrium catch and biomass levels without habitat-quality effects.

Functional forms	Catch (tonnes·year^{-1})	Total biomass (tonnes)	Catch/area (tonnes·km^{-2}·year^{-1})	Total biomass/area (tonnes·km^{-2})
Logarithmic ($\mu(0) = 0.4$)	68 → 126	416 → 1050	3.6 → 6.7	16 → 39
Linear ($\mu(0) = 0.35$)	74 → 135	450 → 1150	3.9 → 7.2	17 → 43
Polynomial ($\mu(0) = 0.34$)	76 → 137	455 → 1170	4.1 → 7.3	17 → 44

Table 2. Single and double habitat-quality effects on fishery catch and total fish biomass.

Habitat-quality effect	Functional forms	Catch (% Δ)	Total biomass (% Δ)	Δ catch/area (tonnes·km^{-2}·year^{-1})	Δ total biomass/area (tonnes·km^{-2})
Single	Logarithmic	+20 → +39	+55 → +92	+0.7 → +2.6	+9 → +36
	Linear	+16 → +31	+47 → +77	+0.6 → +2.2	+8 → +33
	Polynomial	+13 → +25	+40 → +65	+0.5 → +1.8	+7 → +29
Double ($\rho = 0.5$)	Logarithmic	+7 → +15	+74 → +130	+0.25 → +1.0	+12 → +51
	Linear	+4 → +9	+63 → +110	+0.16 → +0.65	+12 → +47
	Polynomial	+1 → +4	+51 → +91	+0.04 → +0.29	+9 → +40
Double ($\rho = 1$)	Logarithmic	–3 → –4	+86 → +156	–0.11 → –0.27	+14 → +61
	Linear	–4 → –8	+70 → +131	–0.16 → –0.58	+12 → +56
	Polynomial	–4 → –12	+55 → +107	–0.16 → –0.88	+9 → +47

lighted the specific contribution of habitat improvements to the fishery by including an explicit habitat-quality function in the marine reserve – fishery model. We have shown that habitat-quality improvements can augment fish biomass and catch levels. The degree to which catch or biomass can increase depends on the nature of the relationship between natural mortality and habitat quality as well as whether the habitat-quality differential influences the rate of fish movement from the reserve to the fishing grounds. However, the sensitivity analysis indicates that habitat-quality improvements from reserve protection are likely to benefit the fishery wherever reserves are established. Only in the case where there is strong restriction to fish movement ($\rho \geq 0.9$) do catches fall, and even then the loss in catch is small. Habitat-quality improvements inside marine reserves can also reduce the exploitation rate at which it becomes profitable for the fishery to establish a reserve.

The greatest benefits to fishery catch from habitat-quality improvements in a marine reserve will be derived from locating the reserve where habitat can recover quickly once protected (an area that is not subject to other stresses such as pollution or sedimentation) and where the fish species respond quickly to these improvements (those with a logarithmic response rather than polynomial). The rate and extent of fish biomass buildup or biodiversity in reserves can be hindered by poor quality habitat (Roberts 2000*a*). High quality habitats are likely to sustain the highest rates of recovery and eventually attain higher biomass or biodiversity than lower quality habitats. However, this has not yet been tested empirically. Though reserves placed in areas of higher habitat quality may perform better (Benaka 1999; Roberts 2000*a*), some of these places may also be prime fishing grounds. Conservation and fishing objectives may conflict in the short term.

The fishery will also benefit if adult and juvenile fish movement is not restricted severely by a habitat-quality gradient. This may be consistent with the idea of protecting an area of lower habitat quality, e.g., one that has been more severely damaged than its surrounding area. If the initial habitat-quality gradient is less than 1 (i.e., $q_1/q_2 < 1$), the improvements in habitat quality in the reserve may lead to q_1 (reserve habitat quality) tending towards q_2 (fishing ground habitat quality) or surpassing it. There is also a conservation argument for protecting lower quality habitats. Protecting these areas may assist their recovery from harmful fishing or other activities. However, tourists are less likely to pay to visit these areas.

Clearly some locations would benefit more from protection than others. For example, we found that heavily exploited fisheries will benefit more from habitat-quality improvements than low exploitation fisheries. However, the absence of perfect knowledge of which locations these are should not prevent the establishment of reserves to protect threatened habitats and fish stocks. Marine reserves have shown significant ecological benefits regardless of the characteristics of the habitat they protect (Conover et al. 2000; Roberts 2000*b*).

Mombasa MNP and the adjacent fishery appear to have all of the right ingredients to benefit from habitat-quality improvements. The results of the simulations are, however, limited by assumptions made, including 50% larval retention and moderate natural mobility of fish ($\sigma = 0.2$). Larval export is thought to be the process by which tropical fisheries can benefit most from marine reserves (Plan Development Team 1990). Other studies of marine reserves assume wide uniform larval dispersal (e.g., Holland and Brazee 1996; Pezzey et al. 2000). If this is the case, in reality, our findings may underestimate the true fishery catch benefits of reserves. However, if fish mobility is zero (not moderate as assumed), the habitat-quality effect on fish movement would also be zero and only the single habitat-quality effect should be considered. Though Lindholm et al. (2001) do not directly investigate the effects of habitat-quality improvement on catch levels, their finding that total juvenile survivorship increases with a reserve is consistent with the finding that catches may be enhanced. However, if fish move into a protected area because of the improvement in habitat quality, as they suggest,

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Fig. 5. Catch levels with single (ρ = 0; open circles), double (ρ = 0.5, crosses), 0.8 (horizontal lines), and 1 (shaded triangles) and without (solid diamonds) habitat-quality effects: (*a*) least effect at low exploitation (10%); (*b*) greatest effect at high exploitation (60%). (Note different scales on *y* axes for *a* and *b*.)

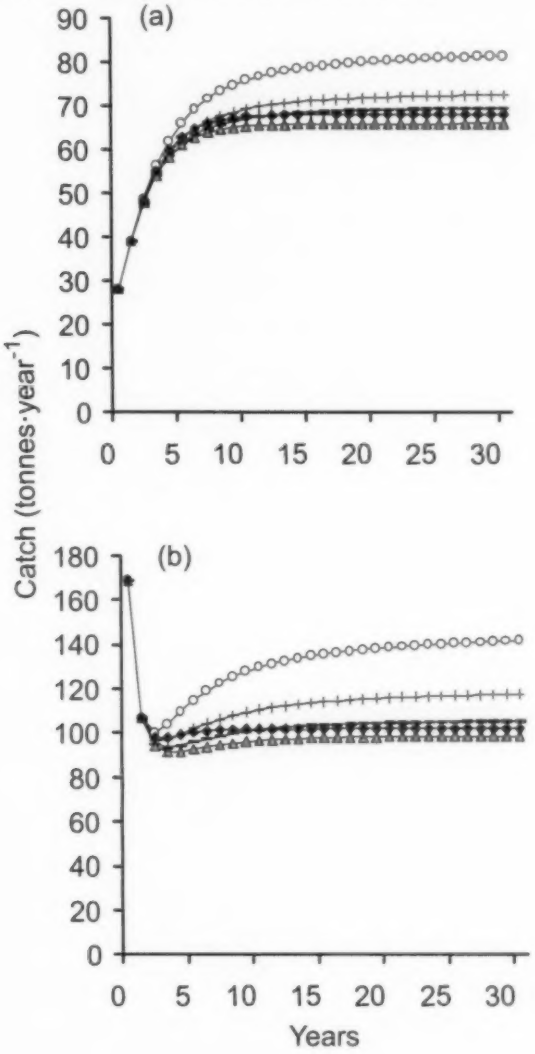
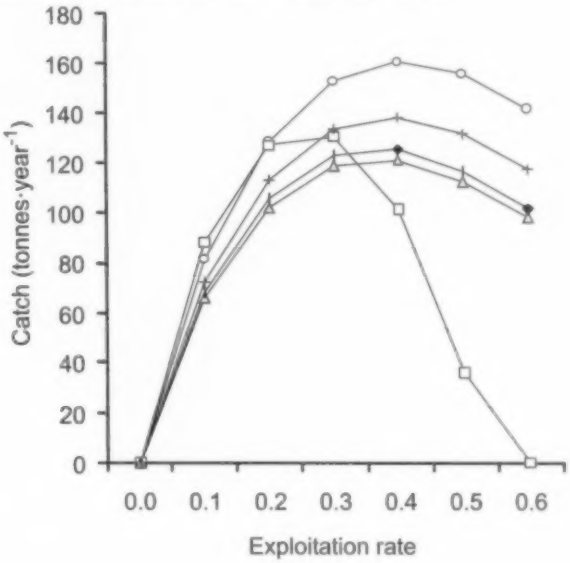


Fig. 6. Steady-state catch levels (30 years) with no reserve (open squares), with single (ρ = 0; open circles), double (ρ = 0.5; crosses), 1 (shaded triangles), and without (solid diamonds) habitat-quality effects. The scenario is one of logarithmic habitat-quality effect, 85% initial growth rate, 40% initial natural mortality (μ = 0.4), and with reserve proportion of 0.3.



there is likely to be a negative impact on catches. This result is wholly dependent on the assumption that movement rates are the inverse of the habitat complexity score. This may well be a plausible assumption for vagile temperate species, but it is less likely to reflect the reality for more sedentary tropical species.

One simplification of this model is the use of aggregated biomass. If complete age- or size-class catch and biomass data were available, the model could have included more detail on the effects of protection (fish and habitat) at various fish life stages. The use of aggregated biomass was appropriate for the data available. It was also used consistently and so should not have produced any biases for or against marine reserve establishment.

As with any study of this nature, there are still many unknowns. However, by modelling a case study site for which some data are available and by simulating various plausible scenarios, we have attempted to ground our model in reality.

The findings support the potential of marine reserves as a valuable ecosystem-based tool that allows both the buildup of fish biomass (as a result of refuge from predation and the increase in reproductive capacity) and habitats to recover from destructive fishing practices or the consequences of ecosystem shifts resulting from fishing. Habitat-quality improvement has been widely ignored in economic studies on marine reserves despite there being much ecological data suggesting that this is an important benefit of reserve establishment. Though precise relationships between fish natural mortality and habitat quality are unknown, our model results indicate that habitat-quality effects should be added to the list of economic, as well as ecological, benefits of marine protection. Depending on the extent to which fish movement is hindered by the habitat-quality gradient between the reserve and fishing grounds, these benefits may manifest themselves in increases in both fishery catches and total fish biomass levels or simply higher fish biomass levels in the reserve. In either case, marine reserves appear to be useful tools in assuring the sustainability of the fishery through both the direct protection of fish species, allowing them to increase in individual size (e.g., McClanahan and Kaunda-Arara 1996; Russ and Alcala 1996) and become more fecund (Sadovy 1996), and the indirect improvement of their essential habitat.

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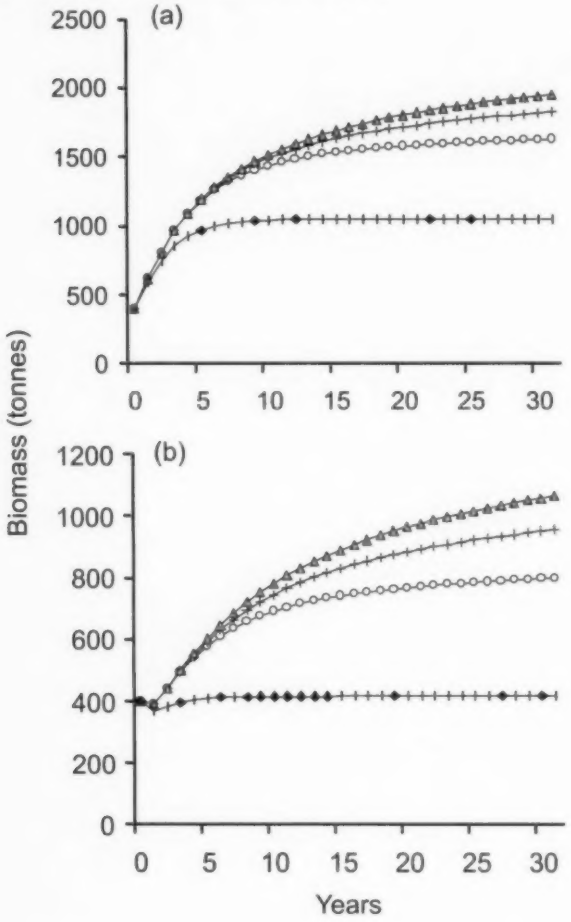
Fig. 7. Total fish biomass levels with single (ρ = 0; open circles), double (ρ = 0.5; crosses), 1 (shaded triangles), and without (solid diamonds) habitat-quality effects: (*a*) least effect at low exploitation (10%); (*b*) greatest effect at high exploitation (60%). (Note different scales on *y* axes for *a* and *b*.)



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Effects of adult common carp (*Cyprinus carpio*) on multiple trophic levels in shallow mesocosms

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Abstract: We examined the effects of adult common carp (*Cyprinus carpio*) on shallow aquatic ecosystems and compared the effects with those of a native benthic fish, channel catfish (*Ictalurus punctatus*). Experimental ponds contained enclosures (0.06 ha) with a low carp biomass (174 kg·ha^{-1}), high carp biomass (476 kg·ha^{-1}), high catfish biomass (416 kg·ha^{-1}), and no fish. We measured abiotic factors (turbidity, suspended solids, total phosphorus), as well as effects on adjacent trophic levels (aquatic macrophytes, zooplankton, and aquatic macroinvertebrates) from July to September. Common carp was positively related to total phosphorus, turbidity, suspended solids, and zooplankton biomass, and negatively related to macrophyte and macroinvertebrate abundance. Suspended solids in the carp treatments consisted primarily of inorganic particles. Carp were either positively or negatively related to phytoplankton, depending on zooplankton abundance. A high biomass of carp had greater effect on nutrients, turbidity, and suspended solids than a low biomass. Channel catfish was positively related to total phosphorus concentrations and altered zooplankton composition, but did not affect turbidity, suspended solids, macroinvertebrates, and macrophytes. These results suggest that common carp have a stronger influence on water quality and aquatic community structure than benthic fish native to North America.

Résumé : Nous avons comparé les effets de la carpe adulte (*Cyprinus carpio*) sur les écosystème aquatiques peu profonds à ceux d'un poisson benthique indigène, la barbue de rivière (*Ictalurus punctatus*). Nos étangs expérimentaux contenaient des enclos (0,06 ha) à faible biomasse de carpe (174 kg·ha^{-1}), à forte biomasse de carpes (476 kg·ha^{-1}) et à forte biomasse de barbues (416 kg·ha^{-1}), ainsi que des enclos sans poissons. Nous avons mesuré les facteurs abiotiques (turbidité, solides en suspension, phosphore total), de même que les effets sur les niveaux trophiques adjacents (macrophytes aquatiques, zooplancton et macroinvertébrés aquatiques) de juillet à septembre. Il y a une relation positive entre la carpe et le phosphore total, la turbidité, les solides en suspension et la biomasse du zooplancton, et une relation négative avec l'abondance des macrophytes et des macroinvertébrés. Les solides en suspension dans les expériences avec les carpes sont surtout des particules inorganiques. La carpe est en relation positive ou négative avec le phytoplancton, selon l'abondance du zooplancton. Une forte biomasse de carpes affecte plus les nutriments, la turbidité et les solides en suspension qu'une faible biomasse. Les barbues sont en relation directe avec les concentrations de phosphore total et elles modifient la composition du zooplancton, mais elles restent sans effet sur la turbidité, les solides en suspension, les macroinvertébrés et les macrophytes. Nos résultats indiquent que la carpe a un effet plus prononcé sur la qualité de l'eau et sur la structure de la communauté aquatique que des poissons benthiques indigènes d'Amérique du Nord.

[Traduit par la Rédaction]

Introduction

The wide distribution and high abundance of common carp (*Cyprinus carpio*) make it a potentially important influence on the primary production and community composition of freshwater systems. Common carp were introduced into the United States as a commercial food fish in the mid-1800s and since have become a wide-ranging exotic species. Common carp, a bottom feeder, should increase the flux of nutrients from the benthic to the pelagic zone of lakes and change the dominant primary producer from submerged macrophytes to phytoplankton. These changes would be especially strong in shallow water systems where a turbidity–macrophyte feedback mechanism regulates water quality (Scheffer et al. 1993). However, it is not clear if common carp, an introduced benthic fish, would have effects qualitatively different from those of native benthivores.

Adult common carp forage on benthic invertebrates and in

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doing so should have effects similar to those of other benthivorous fish. Bottom-feeding fish are considered to be potentially important regulators of aquatic community structure through their direct and indirect influence on water transparency, nutrient recycling, phytoplankton, macrophytes, zooplankton, and benthic macroinvertebrates (Northcote 1988). Many of these hypothesized effects of benthivorous fish come from biomanipulation studies wherein lake or pond parameters are measured before and after the removal of a rough fish population (Meijer et al. 1990*b*; Hayes et al. 1992). These studies have inferred a relationship between benthivorous fish and reductions in benthic macroinvertebrates (Hayes et al. 1992) and increases in turbidity (Meijer et al. 1990*b*). Using these studies to predict the influence of common carp is difficult because their results represent the effects of a mixed-species assemblage. The effects of common carp could differ from those of other bottom-feeding fish either as a result of carp attaining a higher biomass or because carp feed differently by suctioning and expelling bottom sediments (Sibbing et al. 1986).

Across those studies that have either directly or indirectly measured the effects of common carp, some effects are fairly consistent (e.g., reduction of aquatic vegetation (Crivelli 1983); increase in turbidity (Roberts et al. 1995)), whereas other effects are more variable (e.g., nutrient recycling, phytoplankton and zooplankton biomass, macroinvertebrate abundance and diversity). However, none of these previous studies has simultaneously evaluated the effects of common carp on all of these ecosystem components. Many of these environmental variables are very sensitive to changes in other components of the ecosystem (e.g., macroinvertebrates and macrophytes (Crowder and Cooper 1982)); therefore, a simultaneous evaluation of all these components will help to explain the variability of some of the effects of common carp. Part of the uncertainty concerning these effects also comes from the lack of controlled experiments that focus solely on the influence of adult common carp but still retain the complexity of a natural aquatic environment. Few studies have isolated the effects of common carp from those of other fish present in natural systems. Despite the preconception of common carp as harmful to native environments, the strength of their effects has never been compared with those of native benthic fish. This comparison is needed both to validate the investment of effort to control or remove common carp populations and to test the hypothesis that common carp significantly change invaded aquatic communities. To that end, we used mesocosms to quantify the effect of common carp on macrophytes, turbidity, water-column nutrient level, phytoplankton, macroinvertebrates, and zooplankton in shallow-water environments. Our mesocosms allowed us to retain complexity in the form of natural assemblages of aquatic macrophytes, macroinvertebrates, phytoplankton, and zooplankton, while simultaneously allowing us to simplify the fish component of these systems. This approach allowed us to isolate the effects of common carp and to simultaneously examine multiple pathways through which common carp may alter aquatic community structure. We were particularly interested in determining if effects varied with fish biomass and if the effects of common carp were different from those of native benthic fishes. To answer these questions, we used controlled mesocosm experiments to compare the effects of common carp at a high and low biomass and to contrast these effects with those of another common benthic fish, the channel catfish (*Ictalurus punctatus*).

Materials and methods

We placed four enclosures (28 × 19.5 × 1.5 m) into each of four 0.4-hectare, clay-bottom ponds. Each enclosure was a 0.06-hectare rectangle formed by three plastic walls and a shoreline. Nylon-reinforced plastic (18 mm thick) was used for the walls to prevent the exchange of water with the rest of the pond. Before filling the ponds, the base of each plastic wall was pinned and buried 8 cm into the pond substrate. All of the ponds were filled within 24 h of one another from a spring-fed pumping pond, with water filtered to prevent the accidental addition of fish. After the ponds were filled with water, the plastic walls were raised and attached to wooden stakes. Common carp were collected by boat electroshocking from the Fox River, Ill., whereas channel catfish were obtained from a hoop-net commercial fishery on the Mississippi River. Each pond contained four treatments: (1) low carp biomass, 174 kg carp·ha^{-1} (N = 5 fish); (2) high carp biomass, 476 kg carp·ha^{-1} (N = 10 fish); (3) high catfish biomass, 416 kg catfish·ha^{-1} (N = 8 fish); and (4) a control with no fish. Carp biomass was within the range of natural values observed in the wild (113–476 kg carp·ha^{-1}; Panek 1987). To maximize the potential effects of channel catfish and to have a biomass similar to that of carp in the high-biomass treatment, we chose a density of catfish that is at the high end of reported natural abundance for channel catfish (Miller 1966). Within 2 days of filling the ponds, fish were stocked into randomly chosen enclosures within each pond, and the experimental mesocosms were allowed to develop natural benthic, plankton, and vegetation communities for 2 weeks before sampling began. After 70 days, the plastic walls were removed and the ponds were drained to recover the fish. Survival was high for both catfish (97%) and carp (97%), and we observed fish activity in all of the enclosures during the experiment.

We measured water quality in each enclosure every 2 weeks from July to September. Water temperatures and dissolved oxygen concentrations were recorded with a YSI meter. Additionally, we used a clear acrylic tube sampler (1.8 m long) with an interior diameter of 7.3-cm to collect five vertically integrated water samples (7.6–12.5 L·sample^{-1}) per enclosure (DeVries and Stein 1991). The five samples were combined into one integrated sample for the entire enclosure and placed on ice during transport to the laboratory. To determine total phosphorus, a subsample (35 mL) was oxidized with persulfate, an acid molybdate reagent was added, and the absorbance was measured in a spectrophotometer (U.S. Environmental Protection Agency (U.S. EPA) 1994). Chlorophyll *a* concentrations were measured by filtering water (100 mL) with a glass microfibre filter, the chlorophyll was extracted from the filter with acetone, and then the absorbance of the decanted solution was read with a fluorometer (Welschmeyer and Naughton 1994). A turbidimeter was used to determine water clarity by measuring the amount of light scattered from suspended particles in a water sample. Furthermore, the remaining volume from the integrated water sample was used to measure total suspended

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solids and the contribution of inorganic and organic fractions to the total. To determine total suspended solids, water samples were filtered through precombusted and preweighed glass microfibre filters, filters were dried at 90°C for 1 h and weighed on an analytical balance, and then the drying and weighing steps were repeated until a constant weight was determined. The filters were then combusted in a muffle furnace at 500°C for 1 h, cooled for 10 min in a desiccator, weighed, rinsed with distilled water, dried at 90°C, and reweighed to determine the inorganic fraction of the total (U.S. EPA 1994). The organic fraction was determined by subtracting the inorganic fraction from the total weight.

We followed the same collection procedures for zooplankton, combining five tube samples per enclosure for one vertically integrated sample (DeVries and Stein 1991). In the field, the combined water samples were filtered through a 55-μm-mesh plankton net and the zooplankton was preserved in Lugol's solution (U.S. EPA 1994). In the laboratory, zooplankton samples were adjusted to a 100-mL volume and subsampled in 1-mL aliquots. We identified each taxon to suborder or family until at least 200 individuals from each group were enumerated and measured thirty random individuals per taxa with a digitizing pad (Welker et al. 1994). Zooplankton biomass was estimated from length–weight regression equations (Dumont et al. 1975; Culver et al. 1985).

Every 4 weeks, five samples of aquatic macrophytes and macroinvertebrates were collected from each enclosure with a 20-cm-diameter stovepipe sampler (McPeek 1990). Macroinvertebrates were washed from sediments and vegetation into a 500-μm benthos bucket and preserved in 5% formalin solution (U.S. EPA 1994). Individuals were identified to family, enumerated, and measured with an ocular micrometer mounted on a dissecting microscope. Biomass (dry weight) was determined from length–weight regression equations (Smock 1980; G.G. Mittelbach, W.K. Kellogg Biological Station, Michigan State University, Hickory Corners, MI 49060, unpublished data) for all groups except oligachaetes. Because of the difficulty in measuring oligachaete lengths, weights were determined after drying at 80°C for 24 h (U.S. EPA 1994). Percent cover of the bottom by macrophytes was estimated in each enclosure by recording the presence or absence of vegetation at 0.5-m intervals along five equally spaced transects perpendicular to shore. We also identified the aquatic macrophytes present in the stovepipe samples. Diversity of aquatic macrophytes was calculated by the Shannon–Weiner index.

Measurements from one date were not independent from those taken on a previous date, so we analyzed these data with repeated-measures analysis of variance (ANOVA). An individual pond was considered a block, and each enclosure within a pond, a replicate of one of the four treatments. We blocked by pond to remove among-pond variation from tests of treatments, time, and time × treatment interactions. There were no significant block effects ($\alpha = 0.05$) for any of the measured variables. We tested for main effects using a univariate repeated-measures ANOVA, unless the variance–covariance matrix of the data failed a test for sphericity (von Ende 1993). Under these circumstances, we either log-transformed the data or used a repeated-measures multivariate analysis of variance (MANOVA), which is not dependent on the assumption of sphericity. Individual contrasts were established a priori to test for differences between treatments. Statistical significance was judged at $\alpha = 0.05$. All analyses were performed using PROC GLM (SAS 1999).

Results

Total phosphorus concentrations were elevated in the presence of common carp, especially at high carp biomass. The high carp biomass treatment contained higher concentrations of total phosphorus than the low carp biomass (Fig. 1; MANOVA, planned contrast, df = 1,8, $F = 5.51$, $P = 0.05$), channel catfish ($F = 15.24$, $P = 0.005$), and control ($F = 24.58$, $P = 0.001$) treatments. Total phosphorus levels in the low carp biomass enclosure were intermediate, being higher than in the control ($F = 8.33$, $P = 0.02$) but not different from the catfish treatment ($F = 2.96$, $P = 0.12$). From July to early August, water-column nutrient levels were slightly higher in the catfish than in the control enclosures ($F = 6.66$, $P = 0.04$), but not later in the year (Fig. 1; $F = 1.36$, $P = 0.28$). During the experiment, total phosphorus concentrations significantly increased in all of the enclosures (Fig. 1; MANOVA, Pillai's trace, df = 2,7, $F = 6.69$, $P = 0.02$).

At both high and low biomass, common carp had stronger effects on turbidity than channel catfish (Fig. 1). High carp biomass treatment resulted in the highest turbidity, with values larger than those in low carp biomass (Fig. 1; MANOVA, planned contrast, df = 1,8, $F = 6.06$, $P = 0.04$), catfish ($F = 27.68$, $P = 0.001$), and control ($F = 23.59$, $P = 0.001$) treatments. However, even low carp biomass treatment increased turbidity relative to catfish (Fig. 1; $F = 9.57$, $P = 0.02$) and control ($F = 7.01$, $P = 0.03$) treatments. Turbidity in the catfish treatment did not differ from that in the control (Fig. 1; $F = 0.20$, $P = 0.67$).

Common carp increased turbidity through the increase of inorganic suspended particles (Fig. 2), not phytoplankton (Fig. 1). If turbidity were enhanced by high phytoplankton production, total suspended solids would have consisted primarily of an organic fraction. Total suspended solids were highest in the carp treatments and followed similar patterns to turbidity (Fig. 2). The high carp biomass treatment had the highest total suspended solids, with levels marginally higher than low carp (Fig. 2; planned contrast, df = 1,8, $F = 4.13$, $P = 0.08$) and substantially higher than catfish ($F = 17.10$, $P = 0.003$) and control ($F = 16.00$, $P = 0.004$) treatments. The low carp treatment also had a higher concentration of total suspended solids than catfish treatments ($F = 5.40$, $P = 0.05$), with marginally higher concentrations in the low carp biomass than in the control ($F = 4.73$, $P = 0.06$) treatments. Catfish and control treatments did not differ from one another in total suspended solids ($F = 0.02$, $P = 0.89$). Total suspended solids increased over the duration of the experiment in all treatments (Fig. 2; within subjects, df = 4,32, $F = 7.50$, $P = 0.0002$), primarily because of increases in organic suspended solids (Fig. 2; MANOVA, Pillai's trace, df = 4,5, $F = 5.90$, $P = 0.04$). In contrast, no differences in concentrations of organic suspended solids were found between the four treatments (Fig. 2; MANOVA, between subjects, df = 3,8, $F = 0.86$, $P = 0.5$). Inorganic suspended solid concentrations more closely matched the observed turbidity differences (Fig. 2). They were marginally greater in the high carp biomass treatment than in the low carp biomass

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Fig. 1. (*a*) Total phosphorus concentrations ($\mu g \cdot L^{-1}$), (*b*) turbidity (ntu, nephelometric turbidity units), and (*c*) chlorophyll *a* concentrations ($\mu g \cdot L^{-1}$) through time in 0.06-ha enclosures with 29 kg of common carp (*Cyprinus carpio*; High carp, solid circles), 11 kg of common carp (Low carp, open circles), 25 kg of channel catfish (*Ictalurus punctatus*; Catfish, solid triangles), and no fish (Control, open triangles). Data points are mean values ($N = 4$) and the vertical bars represent ±1 standard error.

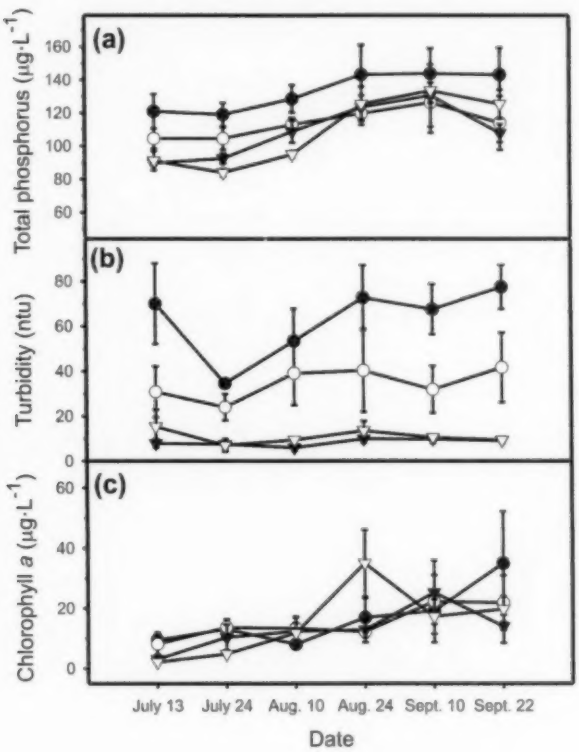
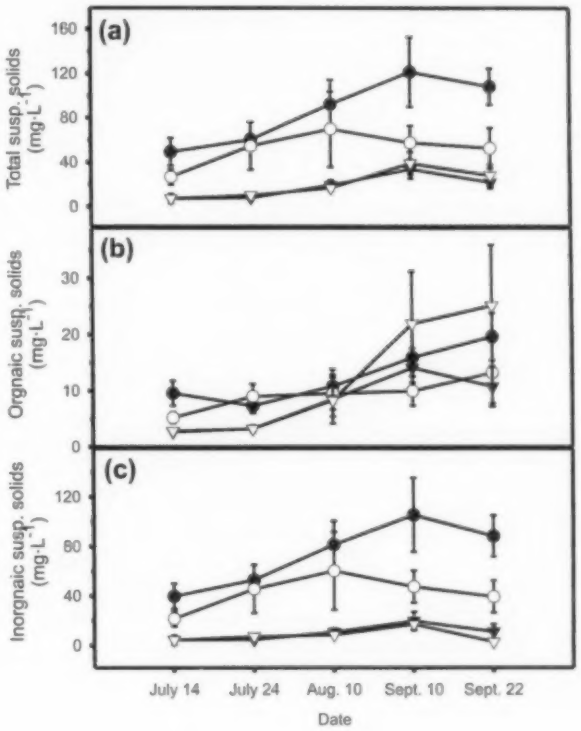


Fig. 2. (*a*) Total suspended (susp.) solids ($mg \cdot L^{-1}$), (*b*) organic suspended solids ($mg \cdot L^{-1}$), and (*c*) inorganic suspended solids ($mg \cdot L^{-1}$) through time in 0.06-ha enclosures with 29 kg of common carp (*Cyprinus carpio*; High carp, solid circles), 11 kg of carp (Low carp, open circles), 25 kg of channel catfish (*Ictalurus punctatus*; Catfish, solid triangles), and no fish (Control, open triangles). Data points are mean values ($N = 4$) and the vertical bars represent ±1 standard error.



treatment (Fig. 2; MANOVA, planned contrast, df = 1,8, $F = 4.09$, $P = 0.08$). Both carp treatments contained higher inorganic concentrations than either the catfish or control treatments ($P \leq 0.05$), which had similar levels of inorganic suspended particles ($F = 0.03$, $P = 0.88$).

Changes in organic suspended solids were reflected in chlorophyll *a* increases in all of the enclosures (Fig. 1; MANOVA, Pillai's trace, df = 2,7, $F = 23.34$, $P = 0.001$). Chlorophyll *a* concentrations were marginally higher in the high carp (Fig. 1; MANOVA, planned contrast, df = 1,8, $F = 4.30$, $P = 0.07$) and substantially higher in the low carp ($F = 5.17$, $P = 0.05$) biomass treatments than in the control. Chlorophyll *a* levels in the catfish treatment were intermediate between the carp treatments (Fig. 1; $P \geq 0.23$) and the control ($F = 0.97$, $P = 0.35$). Total zooplankton biomass was higher in the carp treatments than in the catfish and control enclosures and was not influenced by carp biomass (Table 1). Zooplankton biomass changed significantly with time, rising and then falling in the carp and catfish treatments, while steadily declining in the control (Table 1; within subjects, df = 2,16, $F = 20.96$, $P = 0.001$). However, total zooplankton biomass in the catfish enclosures did not differ from that in the control enclosure (Table 1). Furthermore, total zooplankton biomass changed more extremely in the high carp biomass enclosures than in the catfish treatment ($F = 3.65$, $P = 0.05$), with slight change compared with the control ($F = 2.83$, $P = 0.09$). Total zooplankton biomass changes in the low carp biomass treatment did not differ from those of the catfish ($F = 1.19$, $P = 0.33$) or control ($F = 0.59$, $P = 0.57$) treatments. Unlike zooplankton biomass, total zooplankton density did not show any differences between the four treatments (Table 1) but did vary over time (within subjects, log-transformed, df = 2,16, $F = 6.91$, $P = 0.01$).

Differences in the biomass and density of taxonomic groups of zooplankton were found between the four treatments. Both carp treatments contained a higher cladoceran biomass than in the control treatment (planned contrast, df = 1,8, $P = 0.02$), whereas cladoceran biomass in catfish treatments were intermediate and not different from in either carp or control treatments (Fig. 3; $P \geq 0.14$). Copepod biomass was greater in carp enclosures than in both catfish and control enclosures ($P \leq 0.01$). Differences in copepod biomass were primarily due to

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Fig. 3. (*a*) Cladoceran and copepod biomass ($mg \cdot L^{-1}$) and (*b*) density ($N \cdot L^{-1}$) through time in 0.06-ha enclosures with 29 kg of common carp (*Cyprinus carpio*; High carp, solid bars), 11 kg of carp (Low carp, open bars), 25 kg of channel catfish (*Ictalurus punctatus*; Catfish, shaded bars), and no fish (Control, hatched bars). Data points are mean values ($N = 4$) and the vertical bars represent ±1 standard error.

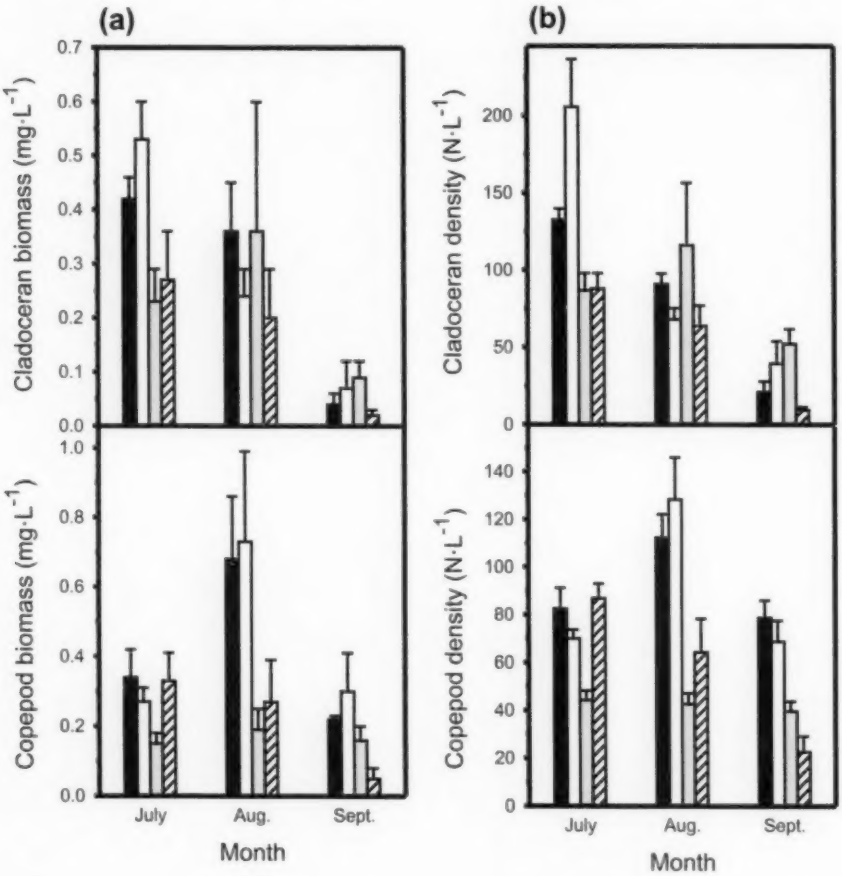

Table 1. Mean total zooplankton biomass ($mg \cdot L^{-1}$ ± 1 standard error (SE)) and density ($N \cdot L^{-1}$ ± SE) in 0.06-ha enclosures with 29 kg of common carp (*Cyprinus carpio*; High carp), 11 kg of common carp (Low carp), 25 kg of channel catfish (*Ictalurus punctatus*; Catfish), and no fish (Control).

	Treatments			
Month	High carp	Low carp	Catfish	Control
Zooplankton biomass				
July	0.79±0.13 a,c	0.88±0.10 a	0.40±0.06 b	0.63±0.15 b,c
August	1.38±0.15 a	1.08±0.21 a	0.61±0.30 b	0.55±0.21 b
September	0.26±0.003 a	0.44±0.21 a	0.31±0.07 a	0.11±0.05 a
Zooplankton density				
July	572.89±84.45 a,c	929.38±292.14 a,c	247.96±43.24 b	676.42±427.38 b,c
August	710.02±196.19 a	565.69±74.70 a	580.02±249.86 a	656.39±303.15 a
September	265.70±81.71 a	413.06±196.59 a	413.95±147.28 a	232.98±139.64 a

Note: Row values with the same letter (a, b, c) are not significantly different (planned contrasts, log-transformed; $P > 0.05$).

calanoid copepod abundance (Fig. 4). The low carp treatment differed from the control in cladoceran ($F = 10.55$, $P = 0.01$) and copepod ($F = 5.55$, $P = 0.05$) density, with a marginal difference in copepod density between high carp and control treatments ($F = 4.33$, $P = 0.07$). Cladoceran densities in catfish treatments were marginally higher than in the control ($F = 4.02$, $P = 0.08$) but not the carp ($P \geq 0.25$) treatments. Copepod densities in both carp treatments were higher than in the catfish treatment ($P = 0.004$). Changes in copepod density over time differed between both carp treatments and the con-

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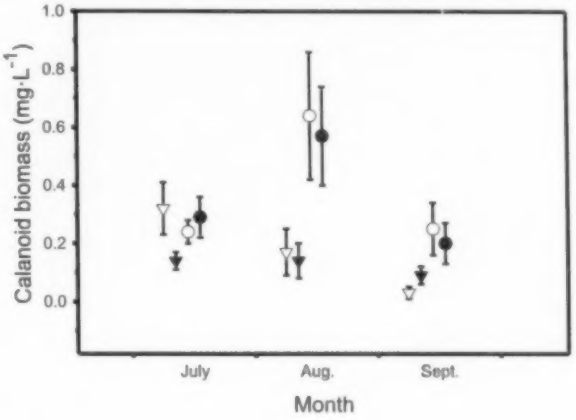
trol, with strongest differences between low carp and control treatments (Fig. 3; within subjects, df = 2,16; high carp biomass vs. control, $F = 3.06$, $P = 0.08$; low carp biomass vs. control, $F = 4.96$, $P = 0.02$). During the experiment, copepod densities rose to a peak in August in the carp treatments, whereas they steadily declined in the catfish and control treatments (Fig. 3).

Aquatic macrophyte cover was highest in the catfish and control treatments, lower in the low carp biomass enclosures, and lowest in the presence of a high biomass of carp (Table 2). Submersed macrophyte abundance was similar between the two carp treatments as well as between catfish and control treatments. During the experiment, macrophyte cover changed over time in all of the treatments (Table 2; within subjects, df = 2,16, $F = 13.38$, $P = 0.0004$). In the high carp biomass treatment, macrophytes declined throughout the entire experiment. In all other treatments, macrophytes increased slightly from July to August, declining only during September (high carp biomass vs. low carp biomass, $F = 6.91$, $P = 0.01$; high carp biomass vs. control, $F = 13.99$, $P = 0.0003$; high carp biomass vs. catfish treatment, $F = 13.39$, $P = 0.0004$). Shannon–Weiner diversity of macrophytes did not differ between the two carp treatments ($F = 5.31$, $P = 0.15$); therefore, we combined the diversity values for high and low carp treatments for comparison with catfish and control treatments. At the beginning of the sampling period, there was no treatment effect on Shannon–Weiner diversity (Fig. 5; $F = 1.57$, $P = 0.26$). In August, Shannon–Weiner diversity was higher in the catfish treatment than in all other treatments (catfish vs. carp, $F = 23.85$, $P = 0.001$; catfish vs. control, $F = 7.04$, $P = 0.03$). By the last sample date, the Shannon–Weiner diversity index was lower in the carp treatments than in both catfish and control treatments (Fig. 5; carp vs. catfish, $F = 15.96$, $P = 0.003$; carp vs. control, $F = 7.80$, $P = 0.02$). Number of macrophyte species was also similar in the high and low carp treatments ($F = 0.36$, $P = 0.61$) and between the catfish and control ($F = 0.21$, $P = 0.68$). When treatments with carp were combined and compared with the combined treatments without carp, significantly fewer macrophyte species were found in the presence of common carp ($F = 33.81$, $P = 0.0002$). Differences in diversity between treatments with and without carp were primarily due to *Chara* species. *Chara* species were found in the control and catfish treatments throughout the entire sampling period but were never present in the two carp treatments. Naiad (*Najas* species), sago pondweed (*Stuckenia pectinata*), and leafy pondweed (*Potamogeton epihydrus*) were present in all treatments. In contrast, sedge (*Carex*) species were temporally variable, being present in the control and low carp treatments in July, only in the catfish treatment in August, and only in the low carp treatment in September.

Macroinvertebrate biomass was reduced by the presence of common carp, but not by channel catfish (Fig. 6). Total macroinvertebrate biomass was lower in both carp treatments than in catfish and control treatments (Fig. 6; planned contrast, df = 1,8, $P \leq 0.01$). Annelid biomass was lower in the high carp biomass treatments than in the catfish (Fig. 6; $F = 35.21$, $P = 0.0003$) and control ($F = 14.97$, $P = 0.01$) treatments, with a similar reduction in the low carp biomass treatment (low carp biomass vs. catfish, $F = 41.32$, $P = 0.0002$; low carp biomass vs. control, $F = 17.19$, $P = 0.003$).

Fig. 4. Calanoid copepod biomass ($mg \cdot L^{-1}$) through time in 0.06-ha enclosures with 29 kg of common carp (*Cyprinus carpio*; High carp, solid circles), 11 kg of carp (Low carp, open circles), 25 kg of channel catfish (*Ictalurus punctatus*; Catfish, solid triangles), and no fish (Control, open triangles). Data points are mean values ($N = 4$) and the vertical bars represent ±1 standard error.



Annelids rose and then fell in abundance in the carp treatments, with the rate of change in the high carp biomass enclosures significantly different than in catfish (Fig. 6; within subjects, df = 2,16, $F = 3.57$, $P = 0.05$) and control ($F = 3.62$, $P = 0.05$) enclosures. Only the high carp treatment significantly reduced chironomid biomass relative to the catfish (Fig. 6; planned contrast, df = 1,8, $F = 17.26$, $P = 0.003$) and the control ($F = 8.81$, $P = 0.02$) treatments. Chironomid biomass declined by the end of the experiment in all treatments (Fig. 6; within subjects, df = 2, $F = 9.44$, $P = 0.002$). Odonate biomass was higher in catfish and control than in the carp treatments (Fig. 6; planned contrast, df = 1,8, $P \leq 0.03$). Odonate biomass increased significantly with time (Fig. 6; within subjects, df = 2, $F = 9.39$, $P = 0.002$) in all treatments except in the low carp biomass treatment, where odonates declined. This pattern of change in the low carp treatment was significantly different than the catfish (Fig. 6; $F = 4.57$, $P = 0.03$) and control ($F = 5.17$, $P = 0.02$) treatments.

Discussion

The use of mesocosms allowed us to control the fish community in our experiment, making it possible to separate the effects of common carp from those of other fishes (e.g., other benthic and planktivorous fish). At the same time, the mesocosms allowed us to retain important natural complexity, such as aquatic macrophytes, that are critical in assessing the responses of other components of the ecosystem. In our experiment, systems without common carp were characterized by clear water, with extensive aquatic macrophyte structure, numerous macroinvertebrate predators, and small-bodied zooplankton grazers. The addition of common carp produced a system with highly turbid, nutrient-rich water, few aquatic macrophytes, low numbers of macroinvertebrate predators, many zooplankton grazers, and abundant phytoplankton. Even though some effects of common carp were stronger at a high biomass of fish, in general, the influence of common carp on

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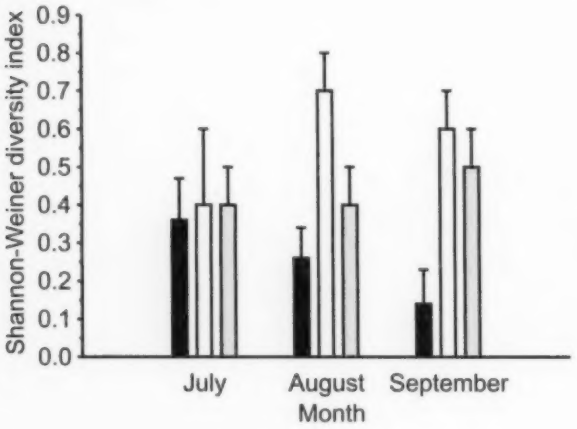
Table 2. Mean (± 1 standard error) percent cover of aquatic macrophytes in 0.06-ha enclosures with 29 kg of common carp (High carp), 11 kg of common carp (Low carp), 25 kg of channel catfish (Catfish), and no fish (Control).

	Treatments			
Month	High carp	Low carp	Catfish	Control
July	67.96±9.98 a	60.30±12.71 a	93.72±1.31 b	93.72±5.14 b
August	46.39±18 a	65.70±15.67 a,c	94.68±2.13 b,c	98.15±1.85 b
September	17.13±8.51 a	44.62±17.66 a	93.93±1.14 b	96.27±2.65 b

Note: Row values with the same letter (a, b, c) are not significantly different (planned contrasts; $P > 0.05$).

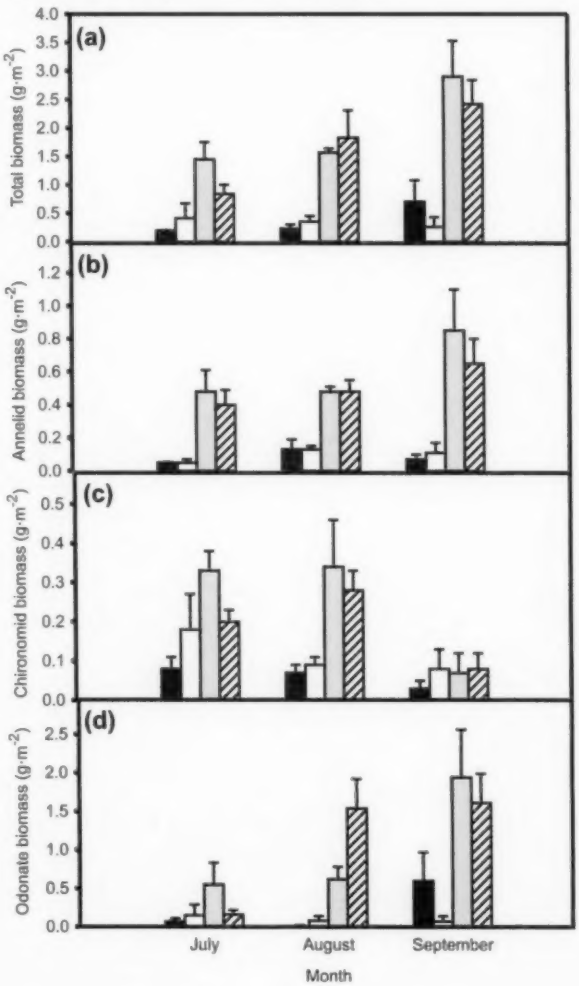
Fig. 5. Diversity of aquatic macrophytes, measured with the Shannon–Weiner index, through time in 0.06-ha enclosures with common carp (*Cyprinus carpio*; solid bars), channel catfish (*Ictalurus punctatus*; open bars), and controls (no fish; shaded bars). Data points are mean values ($N = 7$ for carp treatments and $N = 4$ each for catfish and control) and the vertical bars represent ±1 standard error.



aquatic systems was strong at both low and high fish abundance and distinct from the effects of a native benthic fish.

Common carp increased turbidity, nutrients, and total suspended solids, with largest effects at a high biomass of carp. However, a high biomass of catfish did not have as strong an effect on these variables. Other studies have also found elevated nutrient levels (Lamarra 1975; Lougheed et al. 1998) and turbidity (Cline et al. 1994; Roberts et al. 1995) in the presence of common carp. Studies that have not observed an effect of common carp on turbidity and total phosphorus have suggested that these effects depend on the characteristics of the sediment that the fish are disturbing (Robel 1961; Crivelli 1983; Roberts et al. 1995). Common carp could have increased nutrient concentrations through excretion (Lamarra 1975; Qin and Threlkeld 1990), destruction and subsequent decay of aquatic macrophytes (Carpenter and Lodge 1986), or release of sediment-bound nutrients (Cline et al. 1994). In our study, the large amount of suspended inorganic particles and the adsorption of phosphorus to clay particles suggest that the high turbidity and a large portion of the total phosphorus increase was primarily due to carp disturbance of sediments (Lougheed et al. 1998). Total phosphorus concentrations in channel catfish enclosures were intermediate

Fig. 6. (*a*) Total macroinvertebrate biomass ($g \cdot m^{-2}$), (*b*) annelid biomass ($g \cdot m^{-2}$), (*c*) chironomid biomass ($g \cdot m^{-2}$), and (*d*) odonate biomass ($g \cdot m^{-2}$) through time in 0.06-ha enclosures with 29 kg of common carp (*Cyprinus carpio*; High carp, solid bars), 11 kg of carp (Low carp, open bars), 25 kg of channel catfish (*Ictalurus punctatus*; Catfish, shaded bars), and no fish (Control, hatched bars). Data points are mean values ($N = 4$) and the vertical bars represent ±1 standard error.



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between common carp and control enclosures, suggesting that benthic fish that less actively disturb bottom sediments increase phosphorus primarily through excretion.

Common carp caused increases in nutrients and zooplankton had opposing effects on phytoplankton abundance. Phytoplankton biomass was higher in the presence of common carp, except in August when chlorophyll *a* levels were highest in control treatments. A positive relationship between common carp and phytoplankton production has been observed previously (Meijer et al. 1990*a*; Qin and Threlkeld 1990; Richardson et al. 1990), resulting from either nutrient addition or the suppression of grazing zooplankton. Common carp in our study did not suppress zooplankton, but nutrient levels were high and aquatic macrophyte abundance was low. We did not find an effect of common carp on phytoplankton in previous experiments (J.J. Parkos, unpublished data); however, macrophytes were more abundant in these earlier experiments. When plentiful, aquatic macrophytes can limit phytoplankton production (Scheffer et al. 1993; Hanson and Butler 1994), whereas increased nutrient availability increases phytoplankton abundance (Vanni 1995). Chlorophyll *a* levels in common carp treatments were higher than in the controls primarily during the first two sample periods when pelagic nutrient differences were largest. Later in the summer, when these differences in phytoplankton abundance were reversed, zooplankton grazers were more abundant in common carp treatments than in controls. The dynamic relationship between chlorophyll *a* concentrations, nutrient levels, and zooplankton abundance was also observed in the catfish treatments. Despite the similarity between common carp and channel catfish effects on phytoplankton dynamics, the lack of a strong effect of channel catfish on nutrients resulted in only weak increases in chlorophyll *a* levels beyond controls. If nutrient levels are not elevated, even common carp may not increase phytoplankton abundance (Roberts et al. 1995). Contrary to previous studies, we found that common carp can decrease phytoplankton biomass, most likely because of increases in herbivorous zooplankton. When zooplankton abundance is not elevated, common carp will increase, not depress, phytoplankton abundance (Meijer et al. 1990*a*; Qin and Threlkeld 1990; Richardson et al. 1990). Our results suggest phytoplankton control by both grazers and nutrient availability, with carp-induced effects stronger when macrophytes are less abundant.

The increase in zooplankton abundance in the presence of common carp in our experiment contrasts with previous observations of either carp-associated reductions in zooplankton (Meijer et al. 1990*a*; Richardson et al. 1990; Lougheed et al. 1998) or no effect (Qin and Threlkeld 1990; Cline et al. 1994). Some of these studies used juvenile common carp that would have been primarily planktivorous (total length = 19 mm (Meijer et al. 1990*a*); average standard length = 68.5 mm (Richardson et al. 1990)), explaining the observed reductions in large-bodied zooplankton typical of high planktivore pressure (Carpenter et al. 1985). Higher zooplankton biomass with common carp may have been due to either increases in nutrients and phytoplankton or decreases in larger invertebrate predators. A "bottom-up" effect would have resulted from increased levels of the limiting nutrient, phosphorus, translating into increased availability of phytoplankton to zooplankton grazers. However, common carp had a stronger effect on invertebrate predators, such as odonates, than on phytoplankton. Odonates can prey heavily on zooplankton (Johnson and Crowley 1980) and were less abundant in all carp treatments. Peaks in zooplankton abundance in the presence of common carp coincided with the first large difference between carp and control treatments in odonate biomass, supporting the idea that common carp affect zooplankton primarily through the suppression of invertebrate predators. In studies with weak or no effects of common carp on zooplankton, invertebrate predators were not affected by carp (Qin and Threlkeld 1990; Cline et al. 1994). Therefore, rather than a bottom-up effect, common carp likely have a "top-down" effect on zooplankton by reducing the abundance of important predators.

In contrast, the lack of a decrease in odonates by channel catfish suggests that the catfish-caused increase in zooplankton abundance was due to elevated nutrient and phytoplankton availability. The bottom-up pathway caused by catfish, however, had a weaker effect than the carp-induced top-down effect on zooplankton. Another difference in zooplankton effects between common carp and channel catfish was the positive association between carp and copepods. Only cladocerans showed any increase in abundance from the presence of catfish. Zooplankton in the carp enclosures experienced an environment with high concentrations of inorganic suspended solids, low macrophyte abundance, and few invertebrate predators. Copepods may have an advantage over cladocerans in systems characterized by turbid water and low predator density. The relationship between copepods and environmental conditions is similar to observed reversals in competitive relationships between cladocerans and rotifers in environments with high amounts of suspended clay (Kirk and Gilbert 1990).

Our results support previous findings of common carp causing reductions in macroinvertebrates (Richardson et al. 1990). Annelids, chironomids, and odonates, the three most common macroinvertebrates in our experiment, exhibited reduced biomass levels at both common carp abundances. In a previous experiment, we also observed declines in macroinvertebrate biomass in the presence of common carp, but the decline was not as strong as in the current experiment. This difference in response was most likely due to the higher macrophyte abundance found in the ponds during the previous experiment (J.J. Parkos, unpublished data). The small effect of channel catfish on submerged vegetation may also explain the higher abundance of macroinvertebrates in the presence of catfish as compared with common carp. The lack of a strong negative effect on benthic macroinvertebrates of channel catfish was similar to other native benthivores (Allan 1982). Channel catfish may also have relied on terrestrial insects for a portion of their diet (Miller 1966; McMahon and Terrell 1982). Common carp had a stronger effect on aquatic macroinvertebrates than channel catfish, probably because of the combined effects of predation and habitat alteration. Annelids, mostly oligachaete and hirudinea, were especially affected, most likely as the result of predation. Reductions in odonate biomass were probably due to both predation and loss of aquatic macrophytes. Reductions in macrophyte cover observed in the common carp treat-

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ments would negatively affect odonate species preferentially using aquatic macrophytes as a substrate for attachment (Merritt and Cummins 1996). Our results suggest that the effects of common carp on certain macroinvertebrates will depend on macrophyte abundance, similar to relationships between habitat complexity and fish effects found for centrarchids (Gilinsky 1984) and stream systems (Wooster 1994).

Common carp negatively affected macrophyte abundance by reduction of light availability, increase of siltation rates, ingestion of plant matter, or uprooting during feeding activity. However, there is no evidence that common carp ingest macrophytes to any significant degree (Crivelli 1983; Roberts et al. 1995). In our experiment, *Chara* sp., an example of a submerged plant species with a weak root system (Roberts et al. 1995), was eliminated in the presence of common carp. Greater loss of plants with shallower or weaker root systems supports uprooting as the primary mechanism of macrophyte removal (Crivelli 1983; Fletcher et al. 1985; Roberts et al. 1995). The high amounts of suspended solids and turbidity may also have negatively affected submerged vegetation in the common carp treatments by decreasing light penetration and increasing siltation. Unlike common carp, channel catfish did not affect macrophyte cover, probably because of differences in feeding style. Common carp mouth morphology is designed to burrow into bottom sediments (Sibbing et al. 1986), whereas catfish mouth shape is primarily suited for capture of prey from the sediment surface. By digging into the bottom during feeding, common carp disturb the sediments that hold aquatic macrophyte root systems, resulting in the loss of more weakly rooted plants.

The loss of aquatic macrophytes alone produces many changes in a shallow-water ecosystem (Scheffer et al. 1993). Macrophytes lower turbidity by stabilizing bottom sediments with their roots and by suppressing phytoplankton (Meijer et al. 1990*b*; Scheffer et al. 1993). Macrophytes compete with phytoplankton by shading, using limiting nutrients, providing refuge for grazing zooplankton, and releasing allelopathic substances (Hanson and Butler 1994). Aquatic macrophytes are important to aquatic insects as a refuge from predation (Crowder and Cooper 1982), a source of food for grazers (Carpenter and Lodge 1986), or a place of attachment for eggs, pupae, larvae, or adults (Merritt and Cummins 1996). Loss of macrophytes and increased nutrient loading switches a system from a clear, macrophyte-dominated state to a turbid, phytoplankton-dominated condition (Scheffer et al. 1993). Common carp most consistently affect aquatic macrophytes, nutrient levels, and turbidity. When submerged vegetation is still abundant, however, carp-induced changes in these variables may not translate into significant effects on either plankton or some species of macroinvertebrates.

Native benthic fish, such as channel catfish, do not appear to have as strong an effect as common carp, most likely because of differences in feeding strategy. Common carp had their strongest effect on water quality (turbidity, nutrients) at a high fish biomass, which implies that the most consistent effects of common carp are due to their high abundance in most aquatic ecosystems. However, both a low and a high abundance of common carp altered turbidity, suspended solids, zooplankton biomass, macroinvertebrate abundance, and submerged vegetation cover. This implies that even low densities of adult common carp can have a strong effect on shallow aquatic systems. Furthermore, common carp may especially have a large effect on freshly inundated systems such as flooded backwaters and wetlands. Our pond experiment most closely resembles these conditions because common carp were added shortly after the addition of water. Submerged vegetation may be more vulnerable to turbidity and uprooting when they are first established inside of a newly inundated area. Prevention of early macrophyte establishment will likely stabilize the shallow aquatic ecosystem as a turbid, phytoplankton-dominated state (Scheffer et al. 1993). Increases in turbidity and decreases in macroinvertebrate and macrophyte abundance caused by carp should also negatively affect the growth and recruitment of other fish species. Fish that suffer reduced foraging efficiency under turbid conditions, rely on macroinvertebrates as important prey items, or use aquatic vegetation as spawning substrate, nursery habitat, foraging area, or refuge from predators could all be affected by the presence of common carp. Many fish species use backwaters and wetlands as spawning and nursery habitats; therefore, the strong influence of common carp on these systems may be particularly harmful to native populations.

The most important effects of common carp were not direct predation on aquatic invertebrates but the regulation of freshwater ecosystem structure through feeding activity and nutrient recycling via physical resuspension (Northcote 1988). In this manner, common carp are similar to other fish that regulate food webs through foraging behavior at the sediment layer (e.g., gizzard shad (*Dorosoma cepedianum*; Shaus and Vanni 2000). In shallow aquatic ecosystems, common carp can be considered "ecosystem engineers" (Jones et al. 1994) or "keystone modifiers" (Mills et al. 1993) in that they have strong effects on community composition through their influence on habitat structure. However, common carp may not have equally strong effects on all types of aquatic systems; therefore, prioritization of attempts to control carp should be based on the characteristics of the invaded system. Based on our results, we would predict that common carp cause the largest changes in shallow aquatic systems characterized by easily suspended sediment of high nutrient content, low abundance of firmly rooted vegetation, and regulation of herbivorous zooplankton by invertebrate predators. Consideration of sediment characteristics and submerged vegetation taxa and abundance will especially aid in the prediction of the effects of common carp on aquatic ecosystems. Success of management and restoration efforts in shallow limnetic systems with abundant common carp populations will likely improve when the strong interactions of common carp with community and habitat structure are considered.

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Patterns and correlates of movement and site fidelity in individually tagged young-of-the-year Atlantic salmon (*Salmo salar*)

Stefán Ó. Steingrímsson and James W.A. Grant

Abstract: The literature on stream fish movement offers diverse views on the patterns (restricted vs. nonrestricted), causes (competition vs. habitat use), and consequences (mobile fish of lower vs. equal fitness) of movement. We tagged 320 young-of-the-year Atlantic salmon (*Salmo salar*) (30.1–55.3 mm), using relatively noninvasive tagging (elastomers) and recovery (snorkeling) techniques, to test these alternative views. Most fish (mean = 63.8%) stayed in the study sites (10–120 m) throughout their respective study season (28–74 days). Of the resighted fish, 61.8% moved less than 1 m up- or down-stream and only three fish moved more than 10 m, causing extremely leptokurtic movement curves. Movement and site fidelity were weakly affected by habitat use and competition. Fish originally found in slow water moved farther than fish from fast water, whereas fish found at high population densities were more likely to disappear than fish from low densities. Finally, mobile fish grew as fast or faster than more sedentary fish, supporting the idea that movement can be advantageous and is not just a by-product of density-dependent population regulation.

Résumé : La littérature scientifique sur les déplacements des poissons en eau courante fournit des perspectives diverses sur les structures (confinement vs. ouverture), les causes (compétition vs. utilisation de l'habitat) et les conséquences (poissons mobiles de fitness inférieur vs. fitness égal) des déplacements. Nous avons marqué 320 saumons de l'Atlantique (*Salmo salar*) de l'année et utilisé des techniques relativement inoffensives de marquage (élastomères) et de recapture (plongée en apnée) pour évaluer ces différentes perspectives. La plupart des poissons (moyenne = 63,8 %) sont demeurés aux sites d'étude (10–120 m) durant la durée de leur étude respective (28–74 jours). Parmi les poissons retracés, 61,8 % s'étaient déplacés de moins de 1 m vers l'amont ou vers l'aval et seulement trois poissons avaient parcouru plus de 10 m, ce qui a produit des courbes de déplacement à leptocurtose extrême. L'utilisation de l'habitat et la compétition affectent peu les déplacements et la fidélité au site. Les poissons trouvés au départ en eau lente se déplacent plus loin que les poissons provenant d'eau rapide; de même, les poissons originaires de sites à forte densité de population sont plus susceptibles de disparaître que les poissons de sites à faible densité. Enfin, les poissons mobiles croissent aussi rapidement, sinon plus rapidement, que les poissons sédentaires, ce qui laisse croire que les déplacement peuvent apporter des avantages et qu'ils ne sont pas seulement les résultats indirects d'un contrôle de la population relié à la densité.

[Traduit par la Rédaction]

Introduction

Animal movement provides a behavioural link between individuals and higher-level population processes (Turchin 1998). For individuals, the choice between showing site fidelity or moving longer distances has direct consequences in terms of energetic costs (Forseth et al. 1999), growth (Fraser et al. 2001), susceptibility to predation (Gilliam and Fraser 2001), and mortality (Elliott 1994). At the population level, movement plays a role in the regulation of local density (Chapman 1962), determines the spatial scale over which population regulation occurs (Ray and Hastings 1996), shapes the geographical distribution of populations (Hanski 1998), and indicates to what degree populations are divided into smaller evolutionary units (Fausch and Young 1995).

Because streams can be conceptualized as one-dimensional habitats, stream fishes are good candidates for a quantitative examination of the shape of movement curves (Skalski and Gilliam 2000). Early studies on the movement of stream fishes noted that many fish are sedentary (e.g., Gerking 1959). Recently, however, this "restricted movement paradigm" has been questioned by Gowan et al. (1994), who pointed out that the conclusion of restricted movement is often based on only a fraction of the original fish that are recaptured within small study sites. Hence, studies should also examine movement at larger spatial scales, or monitor fish that immigrate into the study sites, to ensure that mobile fish are represented (Gowan et al. 1994).

Although movements of stream fishes have been studied extensively, the literature has a few notable weaknesses. First,

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only few studies examine movement curves quantitatively (Harcup et al. 1984; Heggenes 1988; Gowan and Fausch 1996), and modeling of these curves is rare (but see Skalski and Gilliam (2000), Rodríguez (2002), and Zabel (2002)). Second, these studies rely invariably on invasive methods, e.g., electrofishing, that can promote relocation out of study sites (Nordwall 1999); we are not aware of any study in which fish are carefully observed as they are released back into their home range. Third, although dispersal has major implications for the survival of young-of-the-year (YOY) salmonids (Elliott 1994), the methodological problem of tagging small fish has led to a bias in the movement literature towards larger fish. To date, most studies on dispersal of YOY salmonids sample fish as they drift by a fixed point in space (e.g., Johnston 1997) but rarely follow tagged individuals over time (but see Shirvell (1994) and Kahler et al. (2001)).

An examination of the causes and consequences of mobility is necessary for the prediction and interpretation of movement patterns (Gilliam and Fraser 2001). For salmonids, the conventional view suggests that competition causes small, subordinate individuals to emigrate during episodes of density-dependent population regulation (Chapman 1962; Elliott 1994). This scenario predicts that (*i*) mobile fish will be smaller and grow slower than resident fish and (*ii*) they will be more likely to abandon areas of high population density where competition is greater. Alternatively, some studies suggest that larger, presumably dominant, fish are more mobile than smaller fish (Armstrong et al. 1997; Gowan and Fausch 2002) and that mobile individuals grow faster than resident fish (Kahler et al. 2001; see Fraser et al. (2001) for a non-salmonid example). In this case, mobility is often thought to be caused by ontogenetic changes in habitat preferences rather than density-dependent competition. Hence, this scenario predicts that (*i*) mobile fish will be larger and grow faster than residents, and (*ii*) as fish grow and shift their habitat preferences (see Morantz et al. 1987), they will be more likely to abandon shallow, slow-running waters. Rarely are both scenarios examined simultaneously (but see Kahler et al. (2001)).

This study describes the patterns of movement and site fidelity in individually tagged YOY Atlantic salmon (*Salmo salar*) in a natural stream. Unlike previous studies on stream fish movement, we rely on relatively noninvasive techniques for the capture and release of fish; individuals were caught with dipnets and carefully released via snorkeling within their original territory. Also, to ensure that mobile individuals are represented along with sedentary fish, we conducted this study at three spatial scales (10, 45, and 120 m) and tagged and monitored fish that immigrated into the study area. Finally, we test simultaneously the two alternative scenarios on the causes and consequences of movement in stream salmonids.

Materials and methods

Study area and study population

Data on movement of YOY Atlantic salmon were collected in 1998, 1999, and 2000 at Catamaran Brook, a third-order tributary of the Little Southwest Miramichi River in central New Brunswick, Canada (Fig. 1). The stream's main channel is about 20.5 km long (mean width = 7.2 m), and it is the subject of a long-term study on the effect of logging on the stream and its biota (Cunjak et al. 1993). The adult Atlantic salmon spawn in late October and November each fall (Cunjak et al. 1993). YOY salmon emerge from the gravel and start foraging in mid-June at about 26 mm in length (Randall 1982). Juvenile salmon remain in the stream for 2–3 years, foraging mainly (>99%) on drifting invertebrates (Keeley and Grant 1995). Because of beaver activity and its influence on the spawning migration of adult fish, YOY salmon were only found in the lowest 7 km of the stream in the three study years (Richard A. Cunjak, Department of Biology and the Faculty of Forestry and Environmental Management, University of New Brunswick, Bag Service 45111, Fredericton, NB E3B 6E1, Canada, personal communication).

All data were collected in the lower reach (Cunjak et al. 1993), the 2-km section upstream from the mouth of Catamaran Brook (Fig. 1). The spatial scale (i.e., spatial extent) of the study area, in this case defined as the continuous stream length over which movement was monitored, varied among the three years (Fig. 1). In 2000, movement was monitored within 10 study sites with a median length of 10 m (range 6–11 m). Because no systematic attempts were made to locate fish in areas between the sites, the spatial scale was deemed 10 m. In 1998 and 1999, movement was monitored within single 45- and 120-m-long study sites, respectively, i.e., the spatial scale was 45 m and 120 m. Notice that in 1999, fish were not tagged in the whole 120-m study site, but the spatial scale was judged to be 120 m because recapture attempts were made in both the tagging and non-tagging zones of the study site (Fig. 1). The study sites were selected to represent a wide range of habitats that also were accessible for snorkeling.

Sampling and tagging protocol

A total of 320 YOY Atlantic salmon were individually tagged over the three study seasons, ranging from 40 fish in 1998, when the tagging protocol was developed, to 216 fish in 1999 (Table 1). Fish were tagged at fork lengths between 30.1 and 55.3 mm (1998, 36.6–55.3 mm; 1999, 33.0–51.3 mm; 2000, 30.1–40.9 mm) and as early as 2–3 weeks after emergence. The initial survey each year was conducted according to the following procedure. An observer (author S.Ó. Steingrímsson) snorkeled upstream through the study site, and when a fish was observed at a foraging station, it was caught using two aquarium dipnets and the location was marked by embedding a numbered flag in the substrate. Each fish was anaesthetized using clove oil (Keene et al. 1998) and fork length was measured with calipers to the nearest 0.05 mm. Fish were then tagged by a subcutaneous injection of a minute amount of fluorescent red, green, or orange elastomer (Dewey and Zigler 1996). Each fish was tagged in two of the following eight positions: the operculum (left and right); the base of the dorsal fin (anterior and posterior); the caudal peduncle (dorsal and ventral); and the base of the pectoral fin (left and right) (positions 1–8, respectively). In 2000, when fish were tagged at a relatively small size, tagging positions on the operculum (1 and 2) were omitted. Upon re-

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Fig. 1. The location of the study sites in the lower reach of Catamaran Brook, New Brunswick, Canada. The inset map in the top left corner shows the location of Catamaran Brook within New Brunswick; the enlarged maps in the bottom right corner of the figure show the study sites in 1998 and 1999 and one of the 10 study sites used in 2000 (labeled 1–10). In 1999, the 120-m-long site consisted of tagging zones in which all fish were tagged and nontagging zones in which fish were only recaptured. The dots show the original location of tagged fish in the three enlarged study sites. The values for the latitude and longitude refer to the main map of the lower reach in Catamaran Brook.

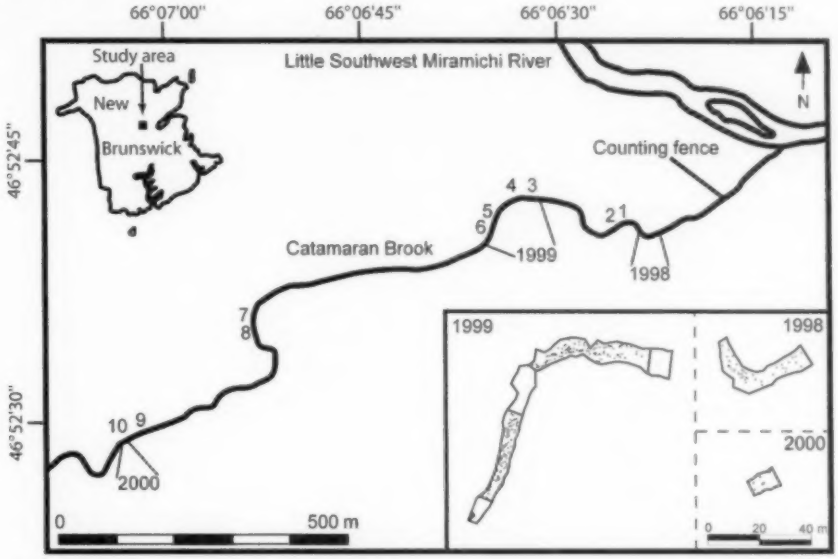

Table 1. Summary of the sampling effort and sampling methods used to monitor movement of young-of-the-year (YOY) Atlantic salmon in Catamaran Brook in 1998–2000.

			Sampling effort[b]			
Survey no.	No. of fish tagged[a]	Survey dates	No. of days	Repeats	Mean water temperature,°C	Survey type
Spatial scale = 10 m, year 2000						
1	64	12–13 July	2	1–3	18.7	Capture
2	—	13 July – 17 Aug.	21	3–5	19.8	Observation
3	—	20–23 Aug.	4	3–5	16.5	Capture
4	—	11–12 Sept.	2	3–5	16.0	Capture
Spatial scale = 45 m, year 1998						
1	40	4–6 Aug.	3	3–5	21.0	Capture
2	—	16–17 Aug.	2	3–5	19.5	Capture
3	—	1–2 Sept.	2	3–5	17.0	Capture
Spatial scale = 120 m, year 1999						
1	187	6–28 July	13	5–7	20.5	Capture
2	—	27 July – 7 Aug.	5	1–3	19.4	Observation
3	29	10–22 Aug.	7	3–5	18.4	Capture
4	—	23–25 Aug.	3	1–3	21.1	Observation
5	—	30 Aug. – 10 Sept.	7	3–5	18.5	Observation
6	—	20–30 Sept.	5	3	11.7	Electrofishing

[a]Twenty-nine immigrants were tagged in 1999; no attempt was made to tag immigrants in 1998 and 2000.
[b]The sampling effort is indicated both as the total number of days allocated towards seeking out YOY salmon and as the estimated number of times (repeats) that each section of the respective study sites was visited (or sampled) during the survey.

capture any fish with fading tags were retagged to minimize tag loss. After fish had recovered from anaesthesia for 5–15 min, they were returned in dipnets to their foraging station via snorkeling, which allowed for observation of the fish during their release. Most fish immediately resumed their natural feeding behaviour when returned to the stream. A few fish, however, appeared disturbed upon release and either hid in, or rested on, the substrate at the point of release or in several cases (<10%) showed bursts of upstream swimming. Fish that swam away were immediately recap-

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tured and placed back on their station to minimize tagging-induced movement; in no case were more than two recaptures necessary.

Data on the location of the tagged fish were collected repeatedly during several sampling surveys conducted from early July to late September (Table 1). The surveys were categorized as (1) capture, (2) observation, and (3) electrofishing surveys (Table 1). In capture surveys, which included the initial tagging effort each year, fish were located via snorkeling, captured, measured, tagged if necessary, and released (see above). In observation surveys, fish were also recognized via snorkeling but only the location was marked. In both these types of surveys, Steingrímsson snorkeled repeatedly through each study site (or a subsection of a site) and often on consecutive days to ensure that a high proportion of the fish were observed (Table 1). However, the time and effort devoted to locating and catching fish varied considerably among the surveys and the study years. Most importantly, in 1999, 13 days were allocated towards the initial tagging effort in an attempt to tag every YOY Atlantic salmon in the tagging zones of the study site; each zone was snorkeled through repeatedly until no new individuals had been found on at least two consecutive occasions. Consequently, later in 1999, untagged individuals observed in the tagging zones were tagged and classified as putative immigrants (Table 1). In 1998 and 2000, less time was devoted to the initial tagging survey as no plans were made to tag all fish in the study sites, e.g., in 2000 only six to eight fish were tagged in each study site. Snorkeling observations were conducted between 1000 and 2200, with over 90% of observations between 1300 and 1900; the mean water temperature in these surveys was 18.8°C (range 15–26°C). Because of low water temperatures, electrofishing was used to catch the study fish in the final survey of the 1999 season. The 120-m study site was divided into eight, 10- to 20-m-long zones, which were blocked with barrier nets. Each zone was sampled by a four-person crew using a Smith-Root Model 12A electrofisher (500 V; Smith-Root, 14014 NE Salmon Creek Ave., Vancouver, WA 98686, U.S.A.), a dipnet, and a seine, held immediately downstream from the shocking area. Three consecutive sweeps were completed for each zone and the final fish number was adjusted for sampling efficiency (Zippin 1958). The study period, from the first day of tagging to the last day of final recaptures, was 30 days in 1998, 87 days in 1999, and 63 days in 2000 (Table 1).

Movement, site fidelity, ecological correlates, and growth

Measurements of individual movements were facilitated by making detailed habitat maps of each study site using an *x*–*y* coordinate system. First, spray-painted nails (25 cm) were driven into both riverbanks at 2- or 2.5-m intervals, linearly along the site length (i.e., *y* transect). After each snorkeling survey, a measuring tape was stretched across the stream between the matching nails on the two riverbanks thus creating an *x* transect at a fixed *y* value (at 0, 2, 4 m, etc.). The *x*–*y* location of each fish were then measured by extending a metre stick at a 90° angle from the measuring tape to the fish location. This method provided accurate (±5 cm) estimates of the *x*–*y* coordinates. Maps with the location of each fish were created for each study site by transferring the data to ArcView GIS 3.2 software. The distance that a fish moved between surveys was measured both as the up- and down-stream distance (along the *y* axis) and as the actual displacement between the two coordinates, a method which also incorporates potential habitat-related movement along the stream width. Because of the length of the study sites in 1998 and 1999, coordinates were recorded in two and three contiguous sections, respectively, which were later transformed into one *x*–*y* surface by applying simple geometric calculations. For each spatial scale, we created movement histograms showing the proportion of the population moving a given distance. Such curves often have to be corrected for the so-called distance-weighting effects as longer distances are less likely to be detected than short movements (Porter and Dooley 1993). However, because we found no statistical difference between the original and the weighted curves (Kolmogorov–Smirnov test, $P > 0.95$ in all cases) and because each pair of corresponding curves looked identical, we only report the original unweighted curves.

Our analysis of the ecological correlates of movement and site fidelity was limited to 1999, because this study season yielded the most comprehensive data in terms of sample size and the number of correlates measured (i.e., population density, fork length, water depth, and current velocity). For each fish, the local population density was estimated by viewing the distribution of individuals in ArcView GIS and was calculated as the number of YOY salmon within a 2-m radius from the fish divided by the circle area within the stream boundaries. The body size estimate was also obtained at a local scale as the relative fork length of the focal fish compared with the average fork length of its four nearest neighbors ($\text{fork length}_{\text{focal fish}}/\text{fork length}_{\text{neighbors}} \times 100$). The water depth and the current velocity were measured for each fish at the exact location of capture; the current was measured at 40% of the water column depth using a Marsh-McBirney meter (Model 201D; Marsh-McBirney, 4539 Metropolitan Ct., Frederick, MD 21704, U.S.A.). The four correlates, as measured in the initial survey, were tested for an association with two dependent variables, the seasonal displacement distance and the site fidelity. The seasonal displacement distance was estimated for fish that remained in the study sites throughout the study season and was simply the distance between the first and last location at which a fish was found. The relationship between the correlates and the displacement distance was examined using a linear regression, a curvilinear (i.e., quadratic) regression, and a backwards step-wise regression analysis with all four correlates (and their quadratic terms). Because the three analyses yielded the same results, only the linear regression statistics are reported. In terms of site fidelity, fish were categorized as those that remained in the study site throughout the season (score = 0) or those that disappeared from the sites during the study season via emigration or mortality (score = 1). Logistic regression was used to test for correlates of site fidelity; again the correlates were tested both in a uni- and multi-variate analyses, and because both yielded the same results, only the former is reported. Because the initial survey in 1999 lasted for 23 days, fork length estimates for these analyses were adjusted for date by regressing the fork length on the day of year and adding the residual length of each fish to the mean fork length (44.7 mm, reached on 15 July) for the survey. Because fork length of YOY fish increased in all three years,

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linearly from the time of tagging to early September, growth rates were calculated as (Fork length$_{final}$ – Fork length$_{initial}$) × (Day of year$_{final}$ – Day of year$_{initial}$)$^{-1}$ (unit = mm·day^{-1}).

The total number of tagged fish in each survey was calculated as $N = N_{found} + N_{not\ found}$, where $N_{not\ found}$ refers to fish that were not found in the survey itself but were found in both a previous and a subsequent snorkeling survey; these extra fish were thus presumed to be in the study site, but inactive, during the survey. The decline in the numbers of tagged fish in the study sites was calculated as the instantaneous daily loss rate (Z') according to the following formula

$$(1) \qquad Z' = -\ln(N_t/N_0)/\Delta t$$

where N_0 and N_t refer to the number of fish at the beginning and the end of the period of interest and Δt is the number of days between the two estimates. In this case, Z' incorporates losses resulting from mortality along with losses such as emigration and tag loss (Ricker 1975). Finally, we had access to water discharge data for Catamaran Brook, collected every hour via a hydrometric gauge maintained by Environment Canada (Cunjak et al. 1993).

Results

Patterns of movement and site fidelity

Despite the small spatial scale, our observations on movement are based on a majority of the tagged fish in our study. Of the 291 YOY Atlantic salmon that were tagged at the beginning of the three study seasons (i.e., original residents), 246 fish were resighted at least once during their respective season. Also, of the 29 immigrants tagged in the study site in mid-August 1999 (i.e., early immigrants), 27 fish were resighted at least once during the rest of the season. In addition to these tagged fish, we also caught a total of 30 untagged fish (i.e., late immigrants) in the tagging zones of our study site during the final electrofishing survey in 1999. It is possible that some fish were inactive in the initial 1999 survey and thus wrongly classified as immigrants. However, based on the proportion of fish not found (13.8%) in the other capture survey in 1999 (survey 3) and the fact that we put 1.86 times more effort (13 vs. 7 days) into the initial survey compared with survey 3 (Table 1), we estimate that we missed only $(0.138)^{1.86} = 2.5\%$ of the YOY salmon (4.8 fish) in the initial survey.

Of the original residents, the resighted fish showed remarkably restricted movement; on average 61.8% of these fish moved less than 1 m up- or down-stream from their original tagging location, whereas 96.9% moved less than 5 m in either direction (Fig. 2). The proportion of fish remaining within a given distance was similar for the three study years, irrespective of the spatial extent of the sites, i.e., 97.8, 96.6, and 96.4% of the fish moved less than 5 m up- or down-stream at a spatial scale of 10, 45, and 120 m, respectively (G test, $G = 0.10$, df = 2, $P > 0.9$). Still, the movement curves and their statistical parameters varied among the study years, mainly because of three fish (one in 1998 and two in 1999) that moved farther than 10 m downstream (Fig. 2; Table 2). First, at a spatial scale of 10 m, where no long movement distances could be detected, no clear pattern emerged in terms of skewness of the movement curves, i.e., after 40 days the curve was skewed towards upstream movements ($P < 0.01$), whereas after 20 and 61 days, skewness was not detected ($P > 0.05$; Table 2). At 45 and 120 m, however, all curves were significantly skewed toward downstream movement (all cases, $P < 0.001$). Second, the movement curves were generally leptokurtic, i.e., they had significantly higher peaks and longer tails compared with a normal distribution, and as with skewness, this pattern was clearer at larger spatial scales. Hence, at 10 m, kurtosis ranged from 1.56 to 3.31 ($P < 0.05$), whereas at 45 and 120 m, kurtosis ranged from 9.41 to 110.40 ($P < 0.001$; Table 2).

Not surprisingly, the maximum dispersal distance of the original residents increased with the spatial extent of the study site, ranging from 6.5 m at a spatial scale of 10 m, to 31.0 m at 45 m, and to 84.9 m at a site length of 120 m (Table 2). The median displacement was low, ranging from only 0.86 to 1.65 m. The median displacement also appeared to increase with time (i.e., days from tagging), but this trend was not significant (Spearman's $r = 0.59$, $n = 9$, $P = 0.094$), perhaps because the pattern was inconsistent among the study years, i.e., there was a significant interaction between time and the study year (analysis of covariance, ANCOVA, $F_{[2,3]} = 14.84$, $P = 0.028$; Table 2). In 1999, the early immigrants moved farther (mean = 1.14 m) than the original residents (mean = 0.66 m) over the last month of the study season (Fig. 3; t test, $t = 2.45$, df = 132, $P = 0.016$).

The number of the original resident fish, tagged at the beginning of each study season ($n = 291$), declined during the three seasons at an instantaneous daily loss rate (Z') of 0.0078; hence, on average, 99.22% of the fish remained in the study sites from one day to the next (Fig. 4). For each of the three years, Z' ranged from 0.0118 in 1998, to 0.0083 in 1999, and to 0.0071 in 2000, but the slopes did not differ significantly (ANCOVA, $F_{[2,7]} = 1.34$, $P = 0.322$; Fig. 4). Because of the low loss rates, 72.3, 54.0, and 65.0% of the original residents remained in the study sites at the end of the 1998, 1999, and 2000 season, respectively. The proportion of early immigrants that remained in the study site from tagging in mid-August in 1999 to the end of the season (21 of 29 fish, $Z' = 0.0077$) was identical to the proportion of the original residents retained over the same period (101 of 152 fish, $Z' = 0.0096$; G test, $G = 0.203$, df = 1, $P > 0.5$). Thus, immigrants were not more likely to disappear from the study site than the original resident fish.

The loss of tagged fish from our sites can be due to tag loss, mortality, or emigration. First, it is unlikely that tag loss contributed much to the overall loss of the tagged fish. In the six surveys in which fish were recaptured, only 2.9% (range 0–4.4%) of the tagged fish were missing a tag from one of the two positions. If we assume that the probability of losing both tags is $(0.029)^2$, then only 0.084% of the fish lost both tags between consecutive capture surveys, and only 0.46 of the 320 tagged fish disappeared as a result of tag loss. Of the 119 tagged YOY salmon that were lost over the three study seasons, we cannot estimate accurately how many fish disappeared as a result of mortality or emigration. However, even the distance-weighted curves, which take into account the low probability of detecting longer movement (Porter and Dooley (1993), see methods), suggest that only about 2.7 and 2.0 individuals moved further than 10 m but remained within a distance of 45 and 120 m in 1998 and 1999, respectively. Hence, if this low frequency is an indica-

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Fig. 2. Movement of YOY Atlantic salmon (*Salmo salar*) in Catamaran Brook monitored at a spatial scale of 10 m (*a*, *b*, *c*; 2000), 45 m (*d*, *e*; 1998), and 120 m (*f*, *g*, *h*; 1999). Positive and negative values on the *x* axes refer to upstream and downstream movement, respectively. The horizontal line and the number at the top of each graph indicates the spatial extent of the study site and the number of days from the initial tagging survey (e.g., 20 days), respectively. Notice that even though the *x* axes range from –100 to 20 m, the probability of detecting a given movement distance decreases gradually in the upstream and downstream direction from 100% at 0 m to 0% at the maximum detectable movement distance of 10, 45, and 120 m (see Porter and Dooley 1993).

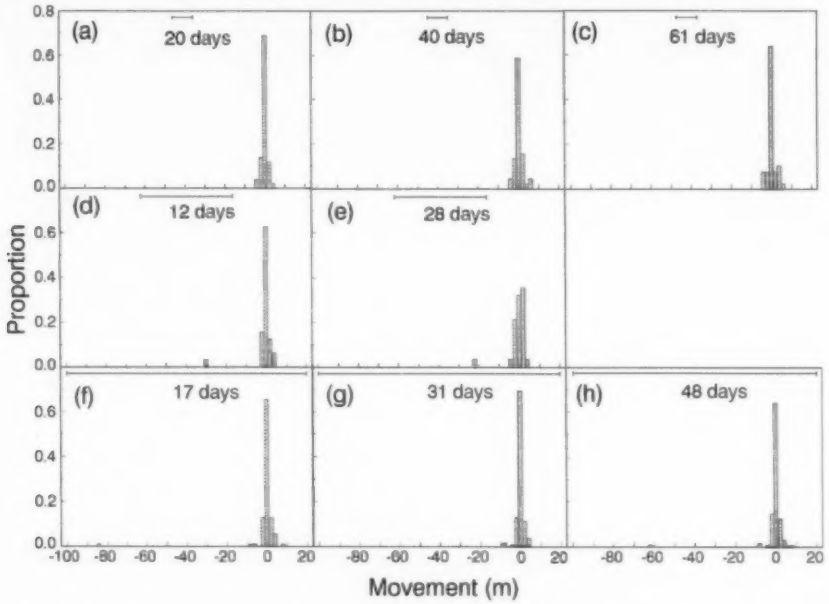

Table 2. Quantitative description of the movement patterns of YOY Atlantic salmon examined at three spatial scales.

Spatial scale (m)	Days from tagging	$N_{found}/N_{not\ found}$[a]	Displacement (m)		Shape of curve[b]	
			Median	Maximum	Skewness (g_1)	Kurtosis (g_2)
Year 2000						
10	20	51/2	0.86	4.22	–0.44ns	2.66***
10	40	44/1	1.03	7.34	1.03**	3.31***
10	61	39/1	1.17	6.50	0.67ns	1.56*
Year 1998						
45	12	32/1	1.16	31.00	–5.14***	28.11***
45	28	28/1	1.65	23.00	–4.37***	21.41***
Year 1999						
120	17	110/50	0.91	84.85	–9.77***	99.97***
120	31	131/21	0.96	8.71	–1.66***	9.41***
120[c]	40	136/10	0.89	62.70	–9.99***	110.40***
120	48	127/12	1.03	61.40	–9.61***	102.56***

[a] N_{found} is the number of original residents found in each survey and is used to establish the movement curves; $N_{not\ found}$ is the estimated number of original residents in the site, but inactive, during the survey.

[b] Skewness (g_1) and kurtosis (g_2) were calculated and tested for normality using Sokal and Rohlf (1981). Significance level: ns, $P > 0.05$; *, $0.05 > P > 0.01$; **, $0.01 > P > 0.001$; ***, $P < 0.001$.

[c] The only curve that is not depicted in Fig. 2.

tor of the frequency of movement outside of the study sites, our data suggest, at least qualitatively, that the majority of the fish were lost to mortality rather than emigration.

Ecological correlates and growth consequences

Of the original residents that remained within the study site throughout the 1999 season, the seasonal displacement was weakly related to current velocity (slope = –0.315, r^2 = 0.085, $P = 0.004$; Table 3). Hence, fish in slow water in the initial tagging survey moved farther from their original location than fish from faster water. The other three variables (population density, relative fork length, and water depth) were not significantly related to seasonal displacement (Table 3). Similarly, only one of the four variables contributed to whether the original residents remained within, or disappeared from, the study site during the season (Table 3). Fish

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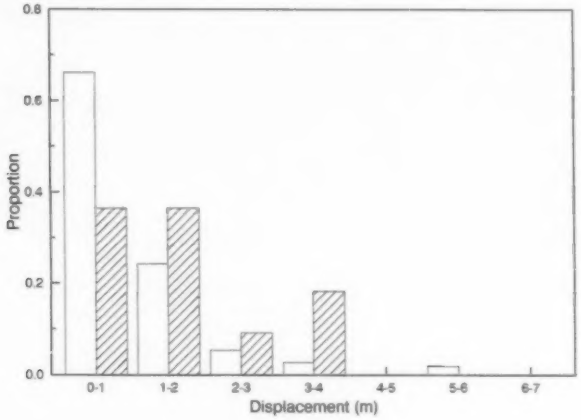
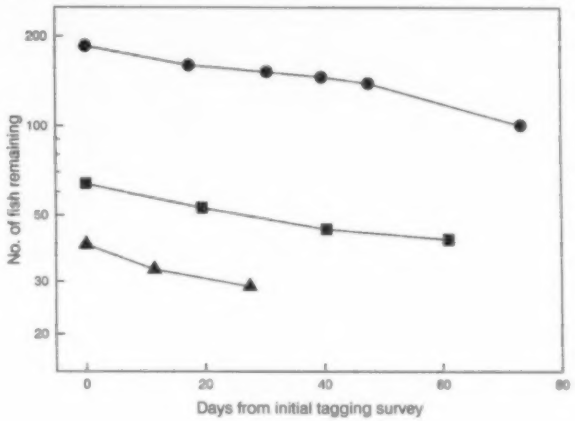
Fig. 3. The displacement of the original resident YOY Atlantic salmon (*Salmo salar*) (open bars, $n = 112$) and the early immigrants (hatched bars, $n = 22$) from mid-August to early September in 1999.



found at high population densities in the initial survey were more likely to disappear from the study site than fish from low-density areas (logistic regression, $B = 1.43$, $P = 0.032$). At a population level, the daily loss rate (Z') calculated between subsequent surveys in the three study years was correlated with the mean water discharge in Catamaran Brook during the corresponding periods (Pearson's $r = 0.814$, $n = 10$, $P = 0.004$), i.e., the original resident fish disappeared faster from the study sites during periods of high discharge (Fig. 5).

Fork length of the original residents increased linearly from the time of tagging to early September each year, and the mean growth rate during this period was 0.295, 0.238, and 0.290 mm·day^{-1} in the 1998, 1999, and 2000, respectively. In 1999, the study season extended to the end of September, whereas growth leveled off sharply in early September; in this case individual growth rates were based only on the original linear increase, and no growth was assumed to have occurred after early September (Girard 2002). For the original residents that stayed in the study sites throughout each of the three seasons, no association was found between individual growth rates and seasonal displacement (all cases, Pearson's correlation, $P > 0.2$). The immigrants found in 1999 provide an alternative view on the growth consequences of movement. When first tagged in mid-August, the early immigrants were slightly, but not significantly, smaller (mean = 51.3 mm) than the original residents (mean = 52.4 mm) (t test, $t = 1.87$, df = 166, $P = 0.063$); a similar pattern was seen for the late immigrants, which were significantly smaller (mean = 53.3 mm) than the original residents (mean = 57.1 mm) when caught at the end of the season (t test, $t = 5.52$, df = 124, $P < 0.001$). In terms of growth, however, early immigrants grew faster (mean = 0.271 mm·day^{-1}) than the original residents (mean = 0.237 mm·day^{-1}) in the latter part of the 1999 season (t test on residual growth rate, $t = 2.65$, df = 105, $P = 0.009$; Fig. 6). In fact, 16 of the 20 immigrants grew faster than the average growth rate predicted for any given initial fork length. Hence, at the end of the season, the early immigrants had reached a similar size (mean = 56.9 mm) to the original residents (mean = 57.1 mm) (t test, $t = 0.48$, df = 113, $P < 0.63$).

Fig. 4. The retention of tagged YOY Atlantic salmon (*Salmo salar*) in the study sites during the three consecutive study seasons: 1998 (▲), 1999 (●), and 2000 (■). The overall loss rate (Z') for the three years was 0.0078 (i.e., slope = –0.0078). For the ease of presentation, the logarithmic y axis is relabeled with the corresponding arithmetic values.



Discussion

The shape of movement curves has been described in several studies on stream-dwelling fish, focusing mostly on salmonids (e.g., Harcup et al. 1984; Heggenes 1988; Gowan and Fausch 1996), cyprinids, and centrarchids (i.e., chub, dace, and sunfish; Smithson and Johnston 1999; Skalski and Gilliam 2000). In this study, most resighted YOY Atlantic salmon moved extremely short distances over their critical first summer of feeding (61.8%, <1 m; 96.9%, <5 m). For periods where longer movements (>10 m) were detected, the movement curves were extremely leptokurtic ($g_2 = 21.41$–110.40), characterized by high peaks and long tails. Although leptokurtosis is a common feature of movement curves reported in the stream fish literature, the frequency of mid- to long-distance movements are higher and kurtosis is less extreme ($g_2 = 1.55$–7.34) than observed in our study (Heggenes 1988; Heggenes et al. 1991; Skalski and Gilliam 2000). As in other studies on YOY salmonids (Hume and Parkinson 1987; Webb et al. 2001), movements were skewed towards downstream in our study.

There are potential methodological reasons for the restricted movement and the extreme leptokurtosis found in our study. First, some of the fish that disappeared in this study may have emigrated out of the study sites, because (*i*) the maximum distance detected each year increased with the spatial extent of the sampling effort, (*ii*) fish moved (immigrated) into the study area in 1999, and (*iii*) the maximum dispersal distance of YOY salmonids is likely about 1 km (Hume and Parkinson 1987; Webb et al. 2001). However, although our movement curves may underestimate longer movements (Porter and Dooley 1993), it is unlikely that further sampling up- and down-stream would have yielded many fish, especially

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Table 3. Ecological correlates of seasonal displacement and site fidelity of YOY Atlantic salmon in Catamaran Brook in 1999.

		Displacement[a]			Site fidelity[b]		
Predictor	Range (min., max.)	Slope	r^2	P	B	% correct	P
Population density (fish·m^{-2})	0.08, 1.19	–0.001	0.000	0.994	1.430	62.57	0.032
Relative fork length (%)	–27.8, 28.2	–0.009	0.023	0.140	0.005	48.13	0.821
Current velocity (m·s^{-1})	0.00, 0.35	–0.315	0.085	0.004	0.202	51.34	0.638
Water depth (cm)	7, 79	0.066	0.001	0.768	–0.034	50.80	0.966

Note: min., minimum; max., maximum.

[a]Results from a linear regression analysis; n = 95 in all four cases. Displacement, current velocity, and water depth were $\log_{10}$ transformed for the analysis.

[b]Results from a logistic regression analysis; site fidelity was scored either as 0 (fish that remained in the study site throughout the study period, n = 95) or 1 (fish that disappeared from the site over the study period, n = 92). Unavoidably, some remaining fish not caught in the final electrofishing survey may be wrongly classified among the disappeared fish; however, a Zippin (1958) estimate of the final number of original residents in the site (n = 101) suggests that this number is low (n = 6).

Fig. 5. The influence of water discharge in Catamaran Brook on the instantaneous daily loss rate (Z') calculated for tagged YOY Atlantic salmon (*Salmo salar*) in the study sites in 1998 (▲), 1999 (●), and 2000 (■). The Z' values are calculated based on the decline in the numbers of fish between each of the consecutive snorkeling surveys.

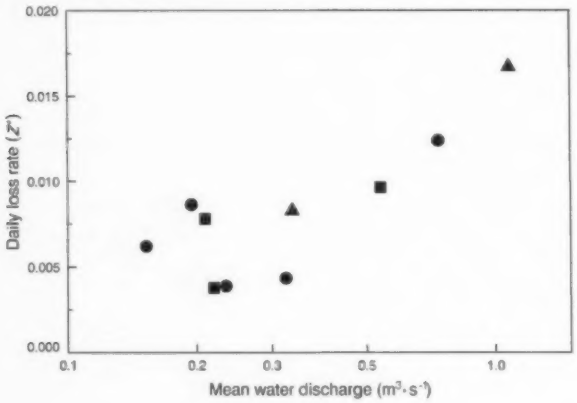
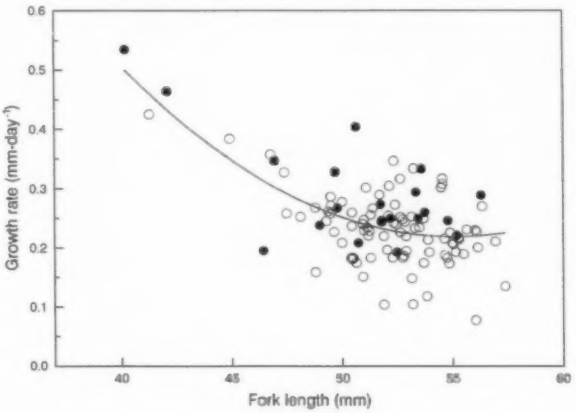


Fig. 6. Growth rate of the original resident YOY Atlantic salmon (*Salmo salar*) (○) and the early immigrants (●) in Catamaran Brook in 1999. Growth rate for all fish was estimated from the time that the early immigrants were tagged (10–22 August) until growth had leveled off (5 September). The x axis refers to the fork length at the beginning of this growth period. The solid line shows the predicted growth rate for any initial fork length and is described by the formula: Growth rate (mm·day^{-1}) = 4.050 – 0.139Fork length (mm) + 0.00126(Fork length^2) (mm) (r^2 = 0.404, n = 107, $P < 0.001$).



considering the low frequency of movement over 10 m. This view is consistent with electrofishing data collected in 1998–2000 at Catamaran Brook, which show an overall decrease in the mean number of YOY Atlantic salmon from 36.4 to 21.2 per 10-m stream length from July to late October, respectively (Z' = 0.50) (based on 13–19 study sites where YOY were found each year; Richard A. Cunjak, Department of Biology and the Faculty of Forestry and Environmental Management, University of New Brunswick, Bag Service 45111, Fredericton, NB E3B 6E1, Canada, personal communication). Hence, if we assume that this loss rate indicates the overall mortality rate in the stream and also applies to our study sites, then 78 of the 119 disappeared fish would be assigned to mortality and only 41 to emigration. Importantly, if fish had been found outside the study sites, the movement curves would have become even more leptokurtic (via longer tails) relative to the curves described in the literature.

Another methodological reason for the low frequency of mid- to long-distance movement observed in our study may be our relatively noninvasive capture and release techniques. In previous studies, fish were often captured via invasive methods, such as electrofishing (Nordwall 1999), and released into the original capture section, the size of which was usually much larger than home range areas of stream fishes and, in particular, those of stream-dwelling salmonids (Nakano 1995). Consequently, many fish were released outside their familiar space, a practice that could promote exploratory behaviour (Armstrong et al. 1997). Occasionally, fish were released close to the site of capture (e.g., Heggenes et al. 1991), but even in these studies, fish were not observed upon their release. In contrast, fish in this study were released at the exact location of capture, and the influence of stress-related movement at the time of release was minimized by catching fish again and bringing them back to their original location.

The classic view of the ecological causes and consequences of movement in YOY salmonids suggests that small, subordinate fish emigrate from areas of high population density (Chapman 1962; Elliott 1994). Our study does not support

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this view; population density was not related to the seasonal displacement of fish and was only weakly correlated with whether or not fish disappeared over the season. Hence, if density induced movements, it did so only by causing movement out of the study site, a process also influenced by density-independent events such as changes in water discharge (Shirvell 1994). In our study, however, the initial local densities ranged from 0.08 to 1.19 fish·m^{-2}, which suggests that territories of the original residents occupied only 1.6–24.5% of the local stream area (Keeley and Grant 1995), a percent habitat saturation (PHS) at which density-dependent emigration, growth, or mortality is only detected in 0.7–46.1% of salmonid populations (see Grant and Kramer (1990) for details on PHS). Consequently, low population densities and low levels of competition may in part explain why the majority of the original residents were sedentary and why the more mobile residents were similar in body size and grew at a rate similar to that of the more sedentary ones.

Alternatively, we suggested that ontogenetic changes in habitat preferences and seasonal habitat changes (e.g., droughts) can cause movement out of areas that become unfavourable and that mobile fish may be larger and grow faster than sedentary fish (Armstrong et al. 1997; Kahler et al. 2001). Thus, YOY Atlantic salmon may leave shallow, slow-running waters as they grow (see Morantz et al. 1987). In this study, fish found in slow currents moved farther from their original location than fish from faster waters, suggesting habitat selection can induce movement. However, current velocity explained only 8.5% of the variation in the displacement distance and did not contribute to whether fish remained in the study area or disappeared. These weak effects can be explained by a parallel study focusing on the habitat use of our study fish in 1999, which showed negligible ontogenetic changes in habitat selection over the first growing season (Girard 2002). Hence, the lack of movement found in this study may reflect the fact that most fish did not outgrow their habitat during the study period. Finally, growth rates of the original residents were independent of how far they moved within the study areas, whereas the immigrants tagged in 1999 grew faster than the original residents from the time they were tagged in mid-August. Hence, our study supports the idea that fish moving longer distances are not necessarily of lower fitness and that movement of stream fish can be advantageous (Fraser et al. 2001; Rodríguez 2002).

Clearly, the perception of mobility depends on the time and space over which movement is monitored. Hence, although the local movement patterns of the original residents changed little over time, there was a gradual increase in the proportion of immigrants in the 1999 study site (to 33.6% of the final fish number), suggesting that on a stream-wide basis a substantial number of fish may relocate longer distances. Similarly, although movement of YOY stream salmonids is often affected by population density (Elliott 1994) and habitat use (Kahler et al. 2001), these effects may vary seasonally from being minimal when movement is restricted in mid-summer to being more profound during periods of intense competition in the days after emergence (Elliott 1994), during drastic habitat changes in early winter (Whalen et al. 1999), or during severe fluctuations in stream discharge (Shirvell 1994). Finally, the restricted movement observed can partly be due to variability among species; Atlantic salmon move shorter distances than many other salmonids such as brook charr (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*) (Rodríguez 2002).

The literature on movement in stream fish frequently classifies individuals as mobile or sedentary based on how far they move or on whether they leave a study site or not. Although this dichotomy is useful for modeling movement (Skalski and Gilliam 2000; Rodríguez 2002), the classification is often arbitrary and may not always reflect fixed differences among individuals in a population (but see Harcup et al. (1984) and Fraser et al. (2001)). In our study, there may be inherent differences between mobile and sedentary fish, as immigrants moved longer distances and grew faster than the original residents after their arrival in the study site. However, the mobility of the immigrants can also be caused by exploratory behaviour as fish settle in new habitats (Armstrong et al. 1997), whereas the fast growth can be due to compensatory growth because the immigrants were slightly smaller than the residents at their arrival in the study site (Maclean and Metcalfe 2001). Finally, although this study suggests that most YOY Atlantic salmon adopt restricted movement soon after emergence, it should be emphasized that mobility of stream fishes varies considerably among life stages and species (Rodríguez 2002). We agree with recent studies that suggest a more rigorous quantitative modeling of movement curves is needed, along with an understanding of the social and environmental conditions that shape these curves in natural habitats (Skalski and Gilliam 2000; Fraser et al. 2001; Rodríguez 2002).

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A simple method for assaying extracellular hydroxyl radical activity and its application to natural and synthetic waters

L.A. Molot, S.A. Miller, P.J. Dillon, and C.G. Trick

Abstract: An assay has been developed to measure extracellular hydroxyl radical (OH*) activity in algal culture media and natural waters over a 4- to 5-day period. The first-order rate constant, k, for loss of absorbance at 590 or 620 nm was determined for erioglaucine, which is sensitive to OH*, insensitive to superoxide and hydrogen peroxide, and stable in the dark and under artificial radiation (280–750 nm) and solar radiation in the absence of oxidants. Variation in irradiance was accounted for by normalizing k with k for a ferric iron reference solution with dye (k/k_{fe}). Trends in k/k_{fe} for streams and lakes were consistent with previous data on photochemical oxidation rates of dissolved organic matter. Values for k/k_{fe} were similar in filtered surface waters of eutrophic Heart Lake and nearby mesotrophic Lake St. George under artificial radiation. Hence, extracellular OH* did not appear to be a direct cause of the onset of a nuisance cyanobacterial bloom in Heart Lake, nor did OH* appear related to the absence of a bloom in Lake St. George. k/k_{fe} was two orders of magnitude higher in algal culture media supplied with 8.8 mM nitrate than in lake waters.

Résumé : Nous avons mis au point une méthode d'analyse qui mesure l'activité extra-cellulaire du radical hydroxyle (OH*) sur une période de 4 à 5 jours dans des milieux de culture d'algues et dans les eaux naturelles. Nous avons déterminé la constante du taux de premier ordre, k, de la perte d'absorbance à 590 nm ou 620 nm pour l'érioglaucine, qui est sensible à OH*, insensible au superoxyde et au peroxyde d'hydrogène et stable à l'obscurité, à la radiation artificielle (280–750 nm) et à la radiation solaire, en l'absence d'oxydants. Les variations de l'irradiance ont été corrigées par une normalisation de k avec le k d'une solution de référence de fer ferrique avec un colorant (k/k_{fe}). Les variations de k/k_{fe} dans les cours d'eau et les lacs sont en accord avec les données antérieures sur les taux d'oxydation photochimique de la matière organique dissoute. Sous un éclairement artificiel, les valeurs de k/k_{fe} sont semblables dans de l'eau de surface filtrée provenant du lac Heart qui est eutrophe et dans l'eau du lac St-George qui est mésotrophe. En conséquence, l'OH* extra-cellulaire ne semble pas être la cause directe du déclenchement d'une prolifération gênante de cyanobactéries dans le lac Heart; l'OH* n'est pas non plus relié à l'absence de prolifération dans le lac St-George. Les valeurs de k/k_{fe} sont une centaine de fois plus élevées dans des milieux de culture d'algues contenant 8,8 mM de nitrate que dans l'eau de lac.

[Traduit par la Rédaction]

Introduction

Photooxidants such as superoxide ($O_2^{\bullet -}$), the hydroxyl radical (OH*), and hydrogen peroxide (H_2O_2) play an important role in dissolved organic matter (DOM) dynamics (Haag and Hoigne 1985; Zepp et al. 1992; Voelker et al. 1997). Their ability to oxidize organic matter is beneficial to some biological communities, but some photoproducts may be harmful. For example, photochemically produced low molecular weight (LMW) organic compounds are substrate for microbial heterotrophs (e.g., Strome and Miller 1978; Amador et al. 1989), but H_2O_2, which may be involved in the production of LMW compounds, can inhibit bacterial production at concentrations as low as 50 nM (Xenopoulos and Bird 1997). In contrast, H_2O_2 appears to stimulate primary production at 100 nM, although algal community responses are highly variable, with some communities harmed by 100 μM and others not (Xenopoulos and Bird 1997). High concentrations above 100 μM were toxic to *Oscillatoria rubescens*, destroying carotenoids and biliproteins (Barroin and Feuillade 1986).

The direct effects of extracellular photooxidants on aquatic life in situ and in the laboratory have not been extensively studied, perhaps because concentrations, production rates, and reaction rates can be difficult to measure. Measurements

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may be hampered by their transient nature, the presence of scavengers such as DOM (Zepp et al. 1992; Brezonik and Fulkerson-Brekken 1998), and interference (e.g., DOM fluorescence can interfere with fluorometric detection methods for H_2O_2). Ecological studies, particularly remote field studies, might benefit from the development of a simple assay for photooxidants that could then be correlated with ecological phenomena. For example, are nuisance cyanobacterial blooms in surface waters correlated with increased levels of extracellular photooxidants? One might expect that surface waters receiving high levels of ultraviolet radiation (UV) would experience high levels of photooxidants and that photosynthetic organisms spending time at or near the surface would be tolerant of both UV and associated photooxidants.

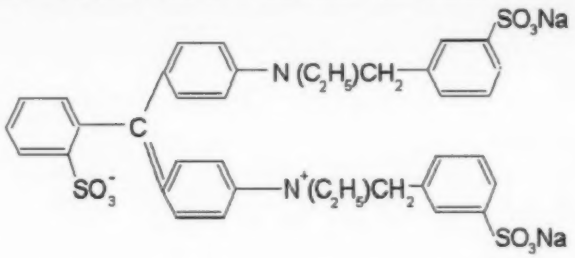
This study presents a relatively simple assay for measuring extracellular photooxidation "activity" as loss of absorbance (photobleaching) of the blue dye erioglaucine in irradiated natural and synthetic water samples. Erioglaucine was chosen because, as shown in this paper, it is stable in the dark and under UV, it is very susceptible to loss of its chromophore by OH* (but not O_2^{*-} or H_2O_2), and it absorbs strongly at 620 nm, a region not masked by high concentrations of humic matter and thus easy to measure spectrophotometrically in natural waters. The assay was applied to a range of natural sites and algal culture media and used to examine whether there is any relationship between nuisance cyanobacterial blooms and extracellular OH*.

Materials and methods

Incubation protocol

Erioglaucine, also known as acid blue 9, Brilliant Blue FCF, Color Index 42090, and Food, Drugs and Cosmetics Blue Dye No. 1, is a triphenylmethane ($C_{37}H_{34}N_2O_9S_3Na_2$; Marmion 1984) with a molecular weight of 792.86 (Fig. 1). Erioglaucine's peak absorbance occurs at 620 nm, with minor peaks at 310 nm (14% of peak absorbance) and 410 nm (13% of peak absorbance). Erioglaucine (Sigma-Aldrich Corp., St. Louis, Mo.; sodium salt, approximately 70% dye) was added to samples to an initial concentration of approximately 8.5 mg·L^{-1}. Absorbance at this concentration was 0.60 at 620 nm (abs_{620} = 0.068concentration + 0.021; R^2 = 1.0, $p < 0.00001$) and 0.26 at 590 nm (abs_{590} = 0.031concentration + 0.000462; R^2 = 1.0, $p < 0.00001$). Absorbance was measured in 1-cm quartz cuvettes daily or every other day at 620 nm or in the shoulder region at 590 nm using a Bausch and Lomb Spectronic 21 spectrophotometer (Thermo Spectronic, Rochester, N.Y.). Samples were incubated in triplicate in the dark and under artificial and natural radiation in 180-mL sterile polyethylene sample bags (Fisher) typically between 5 and 7 days. The bags presented an exposed surface area of 11.5 × 4.5 cm with a depth of 2.8 cm when filled with 120 mL of sample. Transmission through the bags was measured with a 1 × 3 cm piece of polyethylene in a 1-cm quartz cuvette in air with a Hewlett-Packard diode array spectrophotometer. The bags transmitted 86% at 300 nm, 90% at 340 nm, and 93% at 390 nm. The polyethylene material in the sample bags supplied by Fisher changed towards the end of the project, with transmission decreasing by a factor of 0.95. Experiments after 2 November 1999 used the latter material.

Fig. 1. Chemical structure of erioglaucine (after Marmion 1984).



A 2-mL aliquot was removed from each bag and absorbance was measured. Loss was assumed to be a first order, where $dA/dt = -kA$. The rate constant for chromophore decay, k, is the slope of $\ln(A_t/A_0)$ versus time, where A_t is the absorbance at time t (cumulative incubation time) and A_0 is the initial absorbance. Rate constants after 2 November 1999 were adjusted upwards by 1.05 to account for differences in transmission through the newer polyethylene bags.

Artificial radiation

A broad spectrum of radiation (280–700 nm) was provided in the laboratory by 15 40-W fluorescent lamps affixed overhead, an arrangement that provided a large irradiated area year-round at a very low cost. The 15 lamps consisted of three types of lamps next to each other: a cool-white lamp (Sylvania), followed by an UVA lamp (Phillips F40/BL), and then a UVB lamp (Phillips F40UVB). This lamp sequence was repeated five times. This symmetrical array was designed to provide consistent spectral quality and even intensity over a large area (1.0 × 0.9 m) in the centre of the incubation chamber. The incubator was a wooden frame (1.5 × 1.5 × 0.9 m) enclosing an internal chamber with reflective aluminum sheeting on all four sides to homogenize radiation exposure. A full spectrum between 280 and 700 nm was provided, although the spectral quality was not similar to that of solar radiation. Samples were placed on a plywood platform in the middle of the incubator 38 cm below the lamps. A floor fan limited heat buildup. Irradiance (300–800 nm) in the indoor incubator was measured once with an Ocean Optics SD1000 dual-channel spectrophotometer fitted with a deep-well probe for measuring overhead radiation. The decline in lamp intensity was evaluated by periodically assessing loss of absorbance in solutions of deionized water with 0.89 μM ferric chloride.

Outdoor incubations

Several incubations were conducted out-of-doors under solar radiation during the ice-free season. Water from a storm retention pond on the York Campus, Stong Pond, was incubated on a flat roof 30 September – 12 October 1999 at York University (Toronto, Ont.). The samples were placed in a shallow tray in an unshaded site. Outdoor incubations of stream and lake samples collected near Dorset, Ont., in the summer of 2000, were run at the Ontario Ministry of Environment's Dorset Environmental Science Centre (45°13′N, 78°56′W; 200 km north of Toronto). Dorset samples were

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incubated in a shallow water bath (70 × 130 × 9.5 cm deep with a water depth of 3.5 cm) with constant flow-through from a nearby lake to regulate temperature. The water bath did not shade the bags. All natural waters were filtered through a Pall Ultipore nylon filter with a pore size of 1.2 µm before incubation.

Reagents

Photooxidants including OH* were produced in solutions of erioglaucine in deionized water by adding sodium nitrate (Caledon; Haag and Hoigne 1985; Zepp et al. 1987; Brezonik and Fulkerson-Brekken 1998) and ferric chloride hexahydrate (Sigma-Aldrich Corp.; e.g., ligand-to-metal charge transfer and photo-Fenton reactions (Petasne and Zika 1987; Moore et al. 1993; Voelker et al. 1997)). OH* was produced in the absence of radiation by adding 1.8 µM ferrous iron and 10 µM hydrogen peroxide (Fenton reactions). Ferrous sulfate heptahydrate (Sigma), ammonium sulfate (Sigma), and hydrogen peroxide (Sigma) were used. Iron solutions were made on the day that incubations began. All reagents were reagent grade.

O_2^{*-} was generated in a solution of erioglaucine in deionized water in the dark by reacting 6 mL of 1 mM xanthine (Sigma) with 0.2 units of xanthine oxidase (Sigma) in the presence of 1 mM diethylenetriaminepentaacetic acid (DTPA; Sigma; Britigan et al. 1990). DTPA was added to strongly complex iron and prevent OH* formation. The solution was buffered with $Na_3PO_4 \cdot 12H_2O$ to a pH of 7.25. The xanthine – xanthine oxidase reaction forms uric acid, which can be detected by measuring absorbance at 290 nm.

The effects of the following substances on loss of absorbance of erioglaucine in deionized water were examined: Aldrich humic acid at 0–0.71 mM C with 1 mM nitrate; three chelators at 100 µM (sodium ascorbate (Sigma), disodium ethylenediaminetetraacetic acid (EDTA; Caledon), and gallic acid monohydrate (Sigma)) with 0.89 µM $FeCl_3$; Bold 3N algal media, a media used by several of the authors, modified from the original recipe (www.bio.utexas.edu/research/utex/media/media.html) by eliminating soil water and using 0.16 mM P and 8.8 mM nitrate.

Spectral dependence of Fe-mediated loss of absorbance

The effect of wavelength on loss of absorbance of the dye in a solution of 7.1 µM $FeCl_3 \cdot 6H_2O$ was measured in Environment Canada's "Uvator", an incubator with 15 ports to which radiation was directed from a single 1000-W Xenon lamp via mirrors (Desrosiers et al. 1997). Aliquots of the solution were exposed for 5.5 h in sample bags. Glass filters with cutoff wavelengths of 280, 300, 320, 340, and 360 nm were placed above the ports. Radiance between 300 and 360 nm previously measured with an Optronics OL 752 scanning spectroradiometer (Optronics Laboratories, Orlando, Fla.) varied significantly among ports. The percentage loss of absorbance for each port was, therefore, adjusted with a correction factor (mean radiance / radiance of the port).

Study sites

Samples were collected at 2- to 4-week intervals from two small, hardwater, kettle lakes north of Toronto, Heart Lake and Lake St. George. Heart Lake is eutrophic (total phosphorus (TP) levels ranged from 28 to 51 $\mu g \cdot L^{-1}$ with Secchi depth declining to less than 2 m during an *Anabaena* bloom in 1999), whereas Lake St. George has been eutrophic in the past but is now relatively clear and is considered mesotrophic (TP levels ranged from 21 to 33 $\mu g \cdot L^{-1}$ in 1999; however, cyanobacterial blooms do not occur and Secchi depth exceeded 2 m in 1999). Residence times were estimated from $z \cdot A_o / R \cdot A_d$, where z is mean depth, A_o is lake area, A_d is catchment area, and R is mean annual runoff (0.4 m). Day Pond, a small kettle pond located on a farm 7.3 km south west of Lake St. George, was sampled once.

Red Chalk Lake (main basin), Chub Lake, Plastic Lake, and headwater streams Dickie 5 and Dickie 10 are located in the district of Muskoka on the southern edge of the Precambrian Shield in central Ontario. These softwater lakes and streams are described in detail elsewhere (Dillon et al. 1991; Dillon and Molot 1997). The lakes are oligotrophic to mesotrophic headwater lakes with the exception of Red Chalk Lake, which receives discharge from Blue Chalk Lake. Paint Stream is a tributary flowing through the laboratory site (Table 1).

Analytical methods

Total organic carbon (TOC) was measured in samples after filtration through 0.45 µm with a Shimadzu TOC-5000 combustion analyzer except samples from Paint Stream, Red Chalk, and Chub and Plastic lakes. These latter samples were sent unfiltered to the Ontario Ministry of the Environment (MOE) Laboratory where they were acidified, flushed with N_2, oxidized by exposure to UV in acid–persulfate digestion media, and measured colourimetrically with phenolphthalein. The MOE Laboratory analyzed total Fe using inductively coupled plasma–mass spectrometry, total nitrate plus nitrate using an automated hydrazine reduction method, and total phosphorus using ascorbic acid – molybdate colourimetry after autoclave digestion in sulfuric acid (detailed protocols available on request from MOE Laboratory Services Branch, 125 Resources Road, Toronto, ON M9P 3V6, Canada). Photosynthetically active radiation (PAR) between 400 and 700 nm was measured at Dorset with an Eppley pyranometer fitted with a KG-3 filter.

Results

Incubator spectral quality

There were several irradiance peaks at 314, 367, and 436 nm as well as a bimodal peak at 549 and 578 nm. Output was 3.5, 24.9, 6.8, 8.2, and 7.6 $\mu W \cdot cm^{-2}$, respectively, at a central position in the incubator on 28 July 1999 (Fig. 2). Spectral quality and intensity were similar throughout the centre of the incubation chamber. Spectral output from the lamps was relatively low in the region between 315 and 355 nm compared with solar radiation.

Response of dye in dark and under artificial radiation

Absorbance is normally measured at a substance's maximum molar absorptivity, in this case, 620 nm. Although loss of absorbance at 620 nm in solutions with only dye present is small, it is not negligible. Therefore, k for a water sample must be corrected by subtracting k for dye-only solutions. This correction is particularly important when sample k is

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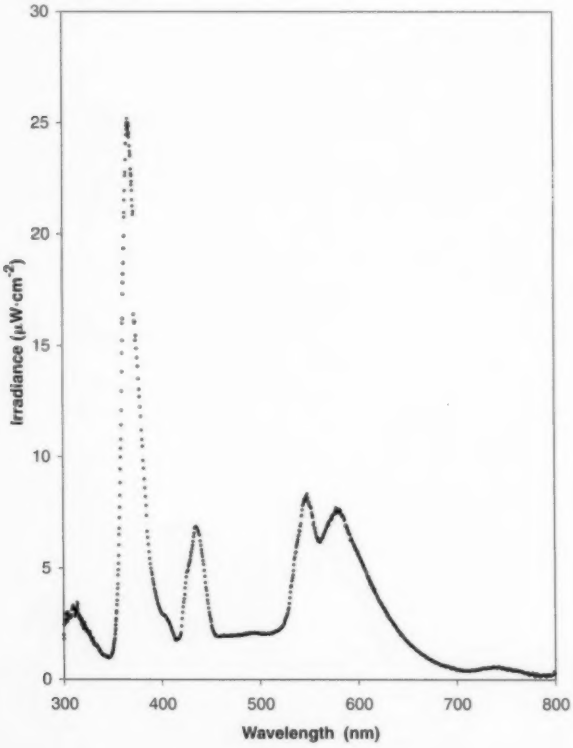
Table 1. Latitude, longitude, residence time, epilimnetic dissolved organic matter (DOM), total phosphorus (TP), total iron (Fe), pH, and nitrate + nitrite (NO_3).

Site	Latitude (N)	Longitude (W)	Residence time, years	DOM, mM C	TP, μM	Fe, μM	pH	NO_3, μM
Red Chalk Lake	45°11′	78°56′	2.6	0.34	0.19	0.11	7.1	0.14
Chub Lake	45°13′	78°59′	2.1	0.45	0.31	0.86	6.0	0.14
Plastic Lake	45°11′	78°50′	4.0	0.17	0.12	0.43	5.7	0.14
Dickie Lake	45°13′	78°59′	1.9					
Epilimnion				0.64	0.19	1.8	6.0	0.14
Hypolimnion				0.63	1.21		5.9	
Lake St. George	43°57′	79°25′	1.2	0.64	0.78		8.3	
Heart Lake	43°45′	79°47′	0.4–0.9	0.79	1.26		8.7	
Day Pond	43°55′	79°30′	<1	1.01	3.55		9.6	
Stong Pond	43°47′	79°30′	<1		2.83			
Dickie 5 Stream	45°09′	79°05′		2.00		5.7–21.7	4.4–4.9	0.3–0.6
Dickie 10 Stream	45°09′	79°05′		4.53		42.8	4.3	1.4
Paint Stream	45°13′	78°56′		0.62				

Note: Heart Lake and Lake St. George data are 1999 summer means for 0- to 3-m composite samples. Other lakes are volume-weighted epilimnetic samples between 13 and 15 July 1999, except Dickie Lake (29 August 2000). Paint Stream, Day Pond, and Stong Pond were sampled once. Dickie 5 and Dickie 10 were sampled on the dates listed in Tables 2–4.

Fig. 2. Irradiance vs. wavelength from artificial radiation used in indoor exposures.



low, for example, in lakes. The need to apply this correction presented a problem because space was limited in the incubator. Hence, absorbance at 590 nm was measured in several experiments to avoid including three bags of dye-only solution. Dye-only solution was quite stable for the duration of the experiment under artificial radiation at this lower wavelength with losses <1% at 590 nm after 35–45 h. In comparison, losses were 5–9% at 620 nm. Values for k in dye-only solutions at 590 nm were less than 1.2×10^{-4} h^{-1} at 590 nm ($R^2 = 0.77$, $p = 0.0002$) and ranged from 6.8×10^{-4} ($R^2 = 0.99$, $p < 0.001$) to 10.8×10^{-4} h^{-1} ($R^2 = 0.85$, $p < 0.0001$) at 620 nm.

Loss of absorbance in deionized water in the dark was negligible. Loss was typically less than 1% of the initial absorbance at 590 and 620 nm over the course of the incubation. Values for the dark k ranged from 0.1 to 0.3×10^{-4} h^{-1} at 590 nm and from 0.4 to 4.1×10^{-4} h^{-1} at 620 nm.

Test of first-order relationship

The relationships between ln(absorbance) and time for all 51 incubations for streams, ponds, and lakes and 0.89 M Fe reference solutions (see Tables 2 and 3) were highly linear, with R^2 values ≥0.92 in all but two (R^2 for these were 0.88 and 0.86). The slopes were also significantly different from zero with $p < 0.0001$. Likewise, all R^2 values were ≥0.90 for 60 rate constants for nitrate, ammonium, EDTA, ascorbate, gallic acid, humic acid, Bold culture media, and Fe additions, except five which were between 0.84 and 0.89. All p values were <0.0001. Therefore, the assumption of first-order kinetics is justified.

Response of dye to oxidants

Erioglaucine was sensitive to iron concentration. After 55 h of irradiation, 10% of absorbance was lost in 0.89 μM Fe and 60% in 8.9 μM Fe at 590 nm. A drop in initial pH from 8.2 to 4.0 (initial pH was adjusted with sodium hydroxide and sulfuric acid, respectively) resulted in a 10-fold increase in k from 10.1×10^{-4} to 97.0×10^{-4} h^{-1}, presumably because acidity inhibits reoxidation of Fe^{2+} to Fe^{3+} by O_2 but not H_2O_2, which, in turn, increases the formation rate of OH* from Fe^{2+} and H_2O_2 (Waite and Morel 1984). These results suggest that erioglaucine is sensitive to one or more of iron-mediated photooxidants (OH*, O_2^{*-}, H_2O_2) and (or) ligand-to-metal charge transfer (Petasne and Zika 1987; Moore et

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Table 2. Relative erioglaucine photobleaching rate constants, k/k_{fe}, measured at 590 and 620 nm in 1.2 µm filtered surface waters uncorrected and corrected for dissolved organic matter (DOM) quenching under artificial radiation.

Absorbance	Date	Site	DOM, mM C	k/k_{fe} Uncorrected	k/k_{fe} Corrected
590 nm	4 May 1999	Dickie 10			
		pH 4.3		0.89	3.47
		pH 7.3		0.18	0.69
	9 July 1999	Plastic Lake	0.26	0.14	0.29
	9 July 1999	Red Chalk	0.34	0.15	0.36
	9 July 1999	Chub	0.45	0.09	0.25
	29 July 1999	Day Pond	1.01	0.25	1.30
	30 Sept. 1999	Stong Pond		0.31	
	7 May to 22 Sept. 1999	Lake St. George			
		Mean	0.65	0.25	0.91
		(SD)	(0.07)	(0.04)	(0.19)
	19 May to 5 Oct. 1999	Heart Lake			
		Mean	0.79	0.23	0.96
		(SD)	(0.05)	(0.03)	(0.13)
620 nm	15 Aug. 2000	Dickie 5	2.28	0.79	7.99
	15 Aug. 2000	Dickie 10	4.52	0.62	11.96
	24 Aug. 2000	Dickie Lake			
		Epilimnion	0.64	0.24	0.72
		Hypolimnion	0.63	0.12	0.26
	30 Aug. 2000	Dickie 5	1.71	0.69	5.33
	30 Aug. 2000	Paint Stream	0.62	0.18	0.48

Note: When measured k for 0.89 µM iron in deionized water (k_{fe}) was not available at 590 nm, k_{fe} was estimated from $0.0051 - (1.86 \times 10^{-5})X$, where X is the cumulative number of days of illumination. Measured k_{fe} was available for all 620 nm experiments. k/k_{fe} ratios at 620 nm were also corrected for loss of absorbance in dye-only solutions. DOM in Dickie 10 Stream was assumed to be 0.71 mM on 4 May 1999.

Table 3. Rate constants, k, at 620 nm for several streams and Dickie Lake near Dorset, Ont., incubated outdoors in 2000.

Site	Start date	k, 10^{-3} h^{-1}	k_{corr}/k_{fe}	PAR, $kJ \cdot m^{-2} \cdot day^{-1}$	k_{corr}/PAR, 10^{-5} $m^2 \cdot kJ^{-1}$
Dickie 5 Stream	19 May	5.89		10 704	
	17 July	6.38		10 042	
	15 Aug.	7.27	18.9	9 028	20.0
	30 Aug.	3.20	9.8	6 393	9.5
Dickie 10 Stream	15 Aug.	7.81	34.9	9 028	36.7
Dickie Lake					
Epilimnion	24 Aug.	1.12	1.4	8 766	1.1
Hypolimnion	24 Aug.	0.96	1.2	8 766	0.9
Paint Stream	30 Aug.	0.74	0.9	6 393	0.9

Note: k_{corr} is k corrected for quenching by dissolved organic matter and direct loss of erioglaucine under ultraviolet radiation. Samples were filtered through 1.2 m membrane filters. Photosynthetically active radiation (PAR, 400–700 nm) is mean daily value for the incubation period.

al. 1993; Voelker et al. 1997). The initial pH of an erioglaucine solution was slightly affected by $FeCl_3$. Initial pH was 4.9, 4.8, and 4.6 for 0.89, 7.7, and 9.5 µM $FeCl_3$ solutions, respectively, with an initial absorbance of 0.25 at 590 nm.

The decline in lamp intensity over a 9-month period was evaluated by assessing the decline in k at 590 nm in incubations with 0.89 µM ferric chloride (referred to as k_{fe}). The decline was linear with relative $k_{fe} = -0.0040\text{days} + 1.083$ ($n = 9$, $R^2 = 0.87$, $p = 0.0002$) where "days" is cumulative use and k_{fe} is relative to its value on 17 May 1999. Relative lamp intensity, estimated as relative k_{fe}, declined 10% for each 30 days of cumulative use. Because of declining lamp intensity, k's from different times were compared by normalizing with k_{fe}, i.e., by comparing k/k_{fe}.

The effect of Fenton oxidants (OH* and H_2O_2) was tested in the absence of UV (Pignatello and Baehr 1994) to determine if OH* alone would degrade the chromophore without UV. The response of the dye to the addition of Fenton reagents 10 µM H_2O_2 and 1.8 µM ferrous iron was compared with the addition of 10 µM H_2O_2 and 1.8 µM ferric iron with the UVA and UVB lamps in the incubator turned off (the cool-white lamps were left on) and in the dark. The ratio of k (ferrous/ferric) at 590 nm was high, 37 under cool-white lamps and –27 in the dark (absorbance increased slightly in the dark, which changed the sign). The ferric and ferrous k's

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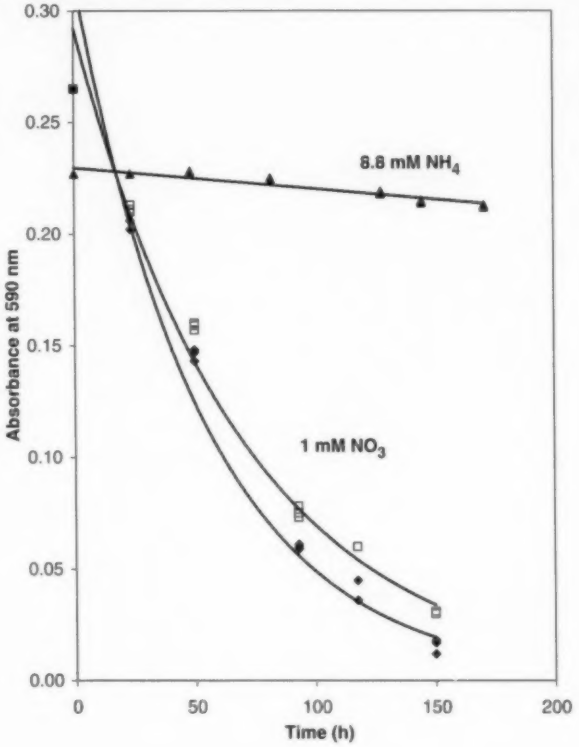
were significantly different at the 1% level (t test comparison of slopes). There was no loss of absorbance with 10 μM H_2O_2 and ferric iron in the dark, suggesting that H_2O_2 does not directly oxidize erioglaucine. Hence, the dye appears sensitive to OH* but not H_2O_2.

Similarly, reaction of 1 mM xanthine with xanthine oxidase in the absence of iron did not cause a loss of absorbance at 620 nm. Therefore, we conclude that erioglaucine is also insensitive to O_2^{*-} at the concentrations generated in this study.

Erioglaucine was also sensitive to nitrate-mediated reactions under artificial radiation but not to ammonium (Fig. 3), suggesting that loss of absorbance at 590 nm was caused by nitrate-mediated formation of OH* (Zepp et al. 1987; Jankowski et al. 1999, 2000). The response of k to nitrate concentration was nonlinear (Fig. 4). Extensive photobleaching occurred at 8.8 mM nitrate, the recommended concentration in Bold 3N algal culture media, with 83% loss of absorbance within 24 h, indicating that substantial extracellular production of hydroxyl radicals can occur in algal media under UV. Dark loss at 8.8 mM nitrate was negligible, with a k of -0.6×10^{-4} ($p = 0.024$) vs. 735×10^{-4} h^{-1} under artificial radiation ($p < 0.0001$). Nitrate-mediated photobleaching was somewhat sensitive to pH in 1 mM nitrate: k was 23% higher at pH 5 than at pH 9.2 (Fig. 3), perhaps because of quenching of hydroxyl radicals by carbonate and bicarbonate ions at the higher pH (Weeks and Rabani 1966; Chen and Hoffman 1973). The difference between the two pH values was significant (t test at 0.1% level). Although carbonate radicals may have been present and reacted with the dye at the higher pH, the decline in k with increasing pH suggests that bicarbonate and carbonate ion quenching exceeds any loss of chromophore from reaction with carbonate radicals.

These results suggest then that erioglaucine is relatively insensitive to H_2O_2, O_2^{*-}, UV, and PAR and that loss of absorbance is caused primarily by OH* when exposed to iron and nitrate in the presence of UV.

Fig. 3. Loss of absorbance of erioglaucine at 590 nm at 8.8 mM ammonium (NH_4; ▲) and 1 mM nitrate (NO_3; ◆, pH 5.0; □, pH 9.2) under artificial radiation.



Estimating quenching by DOM

The ability of DOM to reduce photobleaching of erioglaucine was assessed by adding Aldrich humic acid to 1 mM nitrate solutions under artificial radiation. The relationship between k and DOM concentration in unfiltered solutions was nonlinear over the region 0–0.71 mM C (0–24 mg DOM·L^{-1}) with 74% quenching at 0.71 mM. Because some DOM photoproducts (e.g., organic peroxides and organic radicals) may bleach the chromophore, k represents the net effect of DOM with quenching exceeding photooxidation.

The relationship can be linearized as $k_0/k = 1 + m$[DOM] (Fig. 5), where k_0 is the rate constant for loss of dye without humic acid present and k is the rate constant in the presence of humic acid at some concentration, [DOM]. This is a form of the Stern–Volmer plot where m is the Stern–Volmer constant (4.21 (standard error (SE) = 0.101) and 4.07 (SE = 0.087) L·$mmol^{-1}$ at 590 and 620 nm, respectively). The intercepts are not significantly different from 1.0 ($n = 7$, $R^2 = 1.00$, $p < 0.00001$). Hence, the quenching curves for 590 and 620 nm are virtually identical. Assuming that the quenching behaviour of Aldrich humic acid is similar to the quenching behaviour of natural DOM in situ, then considerable quenching by DOM can occur in fresh waters. For example, a relatively low value of 167 μM C (2 mg·L^{-1}) for northern lakes would quench k by 40%.

Response of dye in algal culture media

Photobleaching of Bold 3N media without iron and nitrate was low at 590 nm ($k = 3.1 \times 10^{-4}$ h^{-1}, $p < 0.0001$; $k/k_{fe} = 0.086$). This is similar to the range measured for dye-only solutions of -0.2×10^{-4} to 1.2×10^{-4} h^{-1} ($k/k_{fe} = 0.059$). Addition of the chelators gallic acid and EDTA at 100 μM with 0.89 μM $FeCl_3$ led to significant increases in k (t test of slopes at the 1% level; $k/k_{fe} = 3.59$ and 2.10, respectively). These results are consistent with the effect of Fe and pH on EDTA removal (Lockhart and Blakeley 1975) and may be a result of photoreduction of Fe^{3+} to Fe^{2+} via ligand-to-metal charge transfer (Miles and Brezonik 1981). Thus, chelators, which are often added to algal culture media, could increase the extracellular OH* formation rate in unbuffered media. Addition of 100 μM ascorbate, an antioxidant in biological systems (Niki 1993; Larson 1997), with 0.89 μM $FeCl_3$ reduced k ($k/k_{fe} = 0.77$), but the decline was not significant (t test of slopes at the 5% level). In general, then, extracellular formation rates of photooxidants can be significant in synthetic media, depending on experimental conditions.

Response of dye in natural waters

Having determined that the chromophore is readily affected by OH*, the photochemical activity of natural waters

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Fig. 4. Rate constants (k) for loss of absorbance at 590 nm as a function of nitrate concentration under artificial radiation.

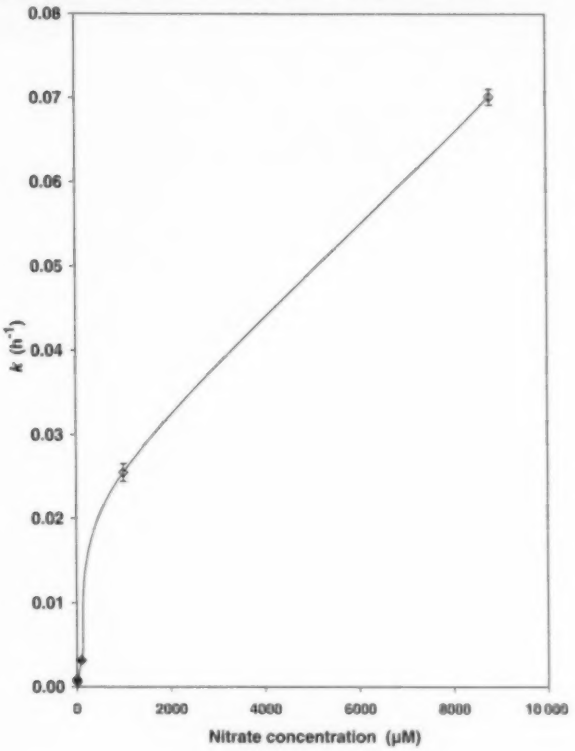
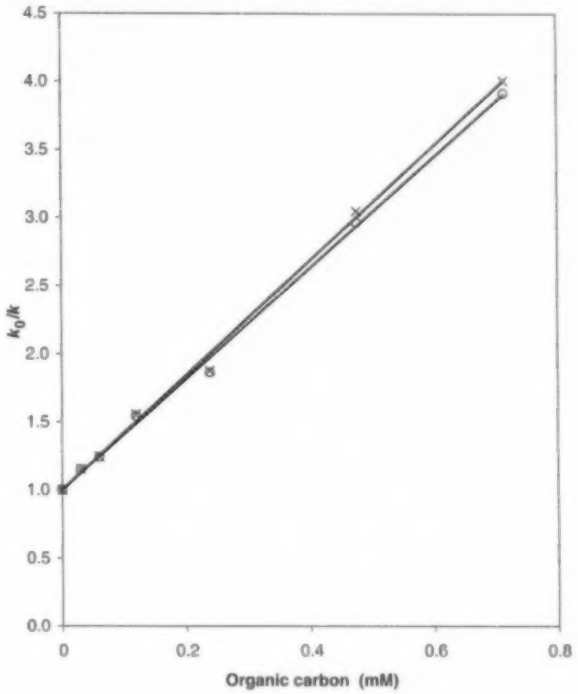


Fig. 5. Stern–Volmer plot of effect of dissolved Aldrich humic acid on loss of absorbance of erioglaucine at 590 (×) and 620 (○) nm in 1 mM nitrate expressed as the ratio of the rate constant at 0 mM organic C (k_0) to k at some concentration of humic acid. Symbols represent means of three replicates.



was assayed by incubating samples with dye under artificial and solar radiation. First-order kinetics adequately described the loss of absorbance in 1.2 μm filtered natural waters under artificial radiation. R^2 for ln(absorbance at 590 nm) versus time was 0.97 in Dickie 10 stream water on 4 May 1999, 0.99 in Lake St. George surface water on 7 May 1999, and 0.97, 0.92, and 0.98 in Plastic Lake, Red Chalk Lake, and Chub Lake surface waters, respectively, on 9 July 1999. Values of k at 590 nm for dark incubations were not significantly different from zero (t test of slopes at 1% level).

Values of k under artificial radiation for several natural waters (filtered through 1.2 μm) normalized for differences in radiation intensity uncorrected (k/k_{fe}) and corrected (k_{corr}/k_{fe}) for DOM quenching are presented (Table 2). Correcting for DOM quenching increased k/k_{fe}. The general pattern for k_{corr}/k_{fe} at both 590 and 620 nm was that high values occurred in acidic stream waters (Dickie 5 and Dickie 10), low values were found in the unproductive softwater Dorset lakes, and intermediate values were found in the hardwater kettle lakes and ponds near Toronto. Titrating Dickie 10 stream water with sodium hydroxide from pH 4.3 to 7.3 lowered k and k/k_{fe} fivefold.

Uncorrected k under solar radiation for three streams and Dickie Lake during the summer of 2000 ranged 10-fold from 0.8×10^{-3} h^{-1} in Paint Stream to 8.0×10^{-3} h^{-1} in a tributary to Dickie Lake, Dickie 5 (Table 3). Values for k_{corr}/k_{fe} (unitless) and k_{corr}/PAR (10^{-5} $m^2 \cdot kJ^{-1}$) were similar, ranging 39- and 41-fold, respectively, with lowest values in Dickie Lake and Paint Stream and much higher values in acidic tributaries to Dickie Lake, Dickie 5, and Dickie 10. PAR and k_{fe} were strongly correlated ($r = 0.74$).

The results for the Dorset streams and lakes are consistent with the direct measurement of photochemical oxidation of stream and lake DOM under solar radiation (Molot and Dillon 1997*a*; Gennings et al. 2001). These studies found that acidity enhances photochemical oxidation rates in stream waters and that photochemical oxidation rates were very low in Dickie Lake and much higher in the Dickie tributaries. Relatively low values in lakes are presumably caused by a number of factors including higher lake alkalinity, lower iron and nitrate concentrations in lakes because of in-lake removal processes (Table 1; Molot and Dillon 1993; Nurnberg and Dillon 1993; Dillon and Molot 1997), and reduced concentrations of absorptive (coloured) DOM (Molot and Dillon 1997*b*).

The relative index, k/k_{fe}, in mesotrophic Lake St. George was similar to that of eutrophic Heart lake (Table 2; Fig. 6). Mean k_{corr}/k_{fe} was fourfold higher than mean k/k_{fe} in both lakes. k/k_{fe} varied over time because of variation in DOM. k_{corr}/k_{fe} was higher in Heart Lake than in Lake St. George by mid-June and remained so until late September. k/k_{fe} did not appear to be a factor in the timing and magnitude of a nuisance cyanobacterial bloom that appeared in Heart Lake in early August (day 210) nor did it appear related to the absence of a bloom in Lake St. George.

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Fig. 6. k/k_{fe} under artificial radiation in Lake St. George (LSG) and Heart Lake (Heart) surface waters as a function of the day of the year in 1999 corrected and uncorrected for quenching by dissolved organic matter. k/k_{fe} is the rate constant divided by the rate constant for a standard solution of erioglaucine in 0.89 μM Fe. ○, Heart uncorrected; □, LSG uncorrected; ●, Heart corrected; ■, LSG corrected.

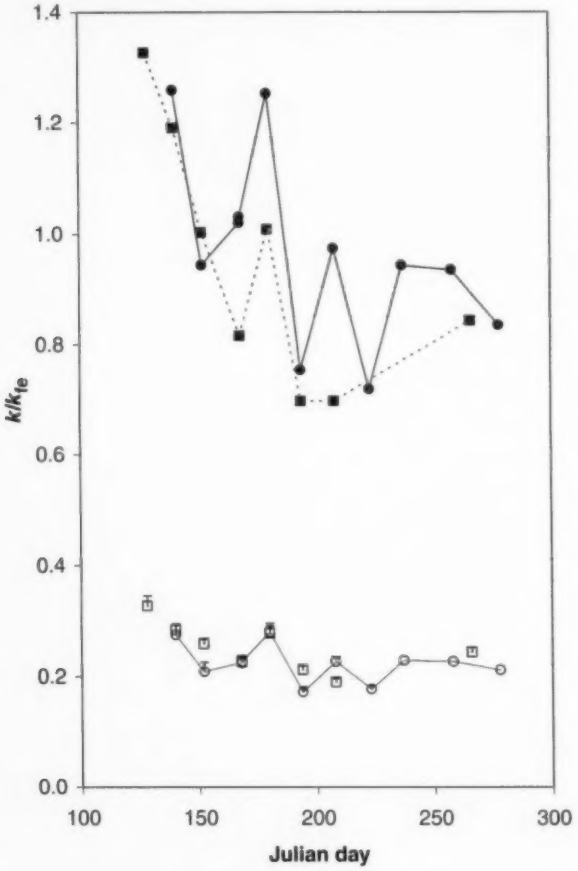
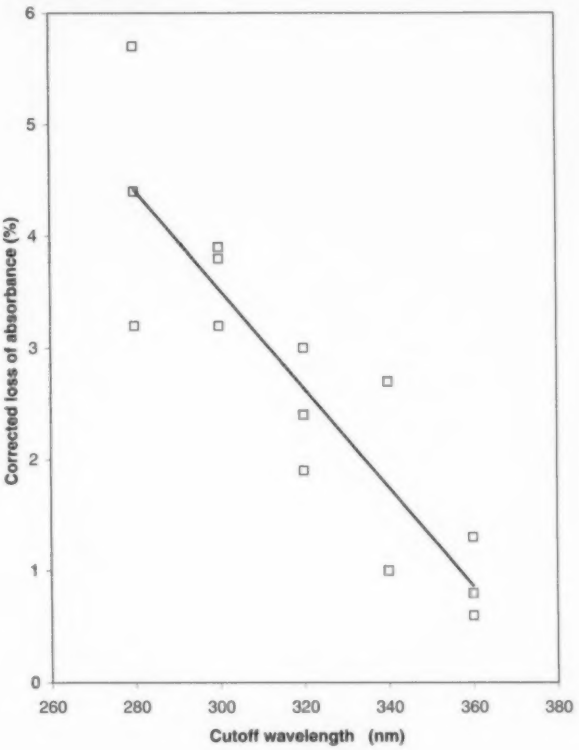


Fig. 7. Loss of absorbance (%) of erioglaucine in 7.1 μM Fe after 5.5 h of exposure to a 1000-W Xenon lamp as a function of cutoff wavelength.



Continuous artificial vs. solar radiation

k reflects the net effect of a variety of processes that produce and consume OH*. Radiation sources differing in spectral quality and quantity can produce different k from identical samples. For example, shorter wavelengths favour production of OH* from iron with loss of absorbance in 7.1 μM $FeCl_3$ exposed to a 1000-W Xenon lamp increasing linearly with decreasing cutoff wavelength between 360 and 280 nm (Fig. 7). Wavelengths above 370 nm produced little effect.

The relative index, k/k_{fe}, for samples obtained with different light sources cannot be directly compared, even when corrected for differences in broadband intensity, unless the sources have similar spectral quality. It is possible in principle to apply spectral weighting functions for each of the photochemical reactions that generate OH* to facilitate comparison of k under different light sources, but this requires detailed photon flux measurements and chemical analyses of the sample in question.

To illustrate the effect of spectral quality, k and k/k_{fe} (measured at 620 nm) under continuous artificial radiation were compared with solar radiation for six stream and lake samples tested in the summer of 2000 (Table 2). Although k and k_{fe} were consistently higher under artificial radiation (Table 4, column A), presumably because of continuous exposure, k_{corr}/k_{fe} in the stream and lake samples were 1.8- to 4.5-fold higher under solar radiation (Table 4, column B). The consistently higher k_{corr}/k_{fe} under solar radiation may reflect the relative paucity of artificial radiation in the region of 315–360 nm.

Discussion

k for erioglaucine appears to be a useful index of extracellular OH* activity in natural and synthetic waters. The dye is stable in the dark, relatively stable under UV and PAR in dye-only solutions, and insensitive to $O_2^{\bullet-}$ and H_2O_2 while sensitive to OH* generated via nitrate-mediated and iron-mediated reactions. Although the dye may also be sensitive to other photoproducts such as carbonate radicals and organic peroxides and radicals, the net effect of increasing DOM and pH (which increases bicarbonate and carbonate ion concentrations) is to reduce loss of chromophore. The degree of OH* quenching by humic acid followed a Stern–

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Table 4. Comparison of rate constants, k, under artificial and natural radiation at 620 nm in 2000.

Date	Sample	$k_{artificial}/k_{solar}$ A	B
15 Aug.	Fe standard	4.4	
	Dickie 5 Stream	1.9	0.4
	Dickie 10 Stream	1.5	0.3
24 Aug.	Fe standard	6.8	
	Dickie Lake epilimnion	4.1	0.5
	Dickie Lake hypolimnion	2.3	0.2
30 Aug.	Fe standard	7.4	
	Dickie 5	4.1	0.5
	Paint Stream	4.7	0.5

Note: Column "A", uncorrected; column "B", k for natural waters first corrected for dissolved organic matter quenching, second corrected for loss of absorbance in deionized water with dye only, and then divided by k for iron standard (k_{Fe}; 0.89 µM Fe in deionized water) to account for differences in radiation intensity.

Volmer relationship, which can be used to estimate OH* activity in the absence of humic acid.

The use of a probe to measure photooxidation activity is not new. Zafiriou and colleagues used the light-dependent loss of NO as a nonselective probe for approximating total free radical production rates with lifetimes greater than 1 ms (Zafiriou et al. 1990; Zafiriou and Dister 1991; Dister and Zafiriou 1993). Several investigators have used organic probes to measure OH* production rates and steady-state concentrations (Zepp et al. 1992; Brezonik and Fulkerson-Brekken 1998; Jankowski et al. 1999) over relatively short time intervals. These methods are much more demanding than the erioglaucine method presented here and generate results that are better suited to mechanistic interpretation (i.e., radical concentrations and production rates over a time period of minutes rather than days). However, the erioglaucine assay is simple to apply, producing absolute k's and relative values when used with a reference solution that span over an order of magnitude in natural waters. k varies with the OH* production potential of the sample, spectral quality and intensity, and the degree of OH* quenching.

The assay has some obvious limitations such as the length of incubation time and the amount added. Nevertheless, the assay should be quite useful for limnologists and biologists studying photochemical and photobiological phenomena because it readily provides an index of OH* activity in natural waters and synthetic media and, therefore, can help examine the ecological roles of extracellular OH*. For example, because relatively high levels of OH* likely occur at the surface of eutrophic waters during the summer, it can be hypothesized that surface-dwelling cyanobacteria that dominate eutrophic communities are able to tolerate OH*, whereas eucaryotic algae are less tolerant. However, k/k_{Fe} (an index of exposure to extracellular OH*) was similar in surface waters of eutrophic Heart Lake and nearby mesotrophic Lake St. George during the summer of 1999, ranging from 0.2 to 0.3 under an artificial UV source. This suggests that extracellular hydroxyl radicals are not a direct cause of the onset of a nuisance cyanobacterial bloom in Heart Lake and that OH* appears unrelated to the absence of a bloom in Lake St. George.

Another example of the assay's utility is the demonstration that a high nitrate concentration, 8.8 mM, in algal culture media causes significant extracellular photoproduction of OH* under artificial UV, with k/k_{Fe} two orders of magnitude higher than in lake waters. To avoid this potentially confounding experimental variable in photobiological studies, researchers might consider using ammonium as an alternative nitrogen source in buffered media.

The values for k in this study correspond in general to the observations of Gennings et al. (2001), who showed that DOM loss rates in streams, measured as first-order constants normalized for variation in UV (a_{uv}), varied 3.5-fold. k/k_{Fe} at 620 nm uncorrected for DOM quenching varied 4.4-fold during the summer of 2000 in four stream samples. In both studies, loss rates were highest in acidic, coloured stream waters and lowest in less acidic lakes, presumably because the lower pH and higher concentrations of iron and nitrate in stream waters enhance photooxidation rates of DOM and dye.

k for loss of absorbance of erioglaucine is related to the OH* concentration by the expression $k = k_{OH,erio}[OH^*_{ss}]_{erio}$, where $k_{OH,erio}$ ($L \cdot mol^{-1} \cdot s^{-1}$) is the rate constant for scavenging of OH* by erioglaucine and $[OH^*_{ss}]_{erio}$ is the pseudo-steady steady-state OH* concentration in the presence of erioglaucine. At steady state, the OH* production rate, P, equals the sum of OH* scavenging by all of the constituents. Although adding erioglaucine increases the rate of scavenging, it does not affect P. Hence,

$$(1) \qquad [OH^*_{ss}] = \frac{[OH^*_{ss}]_{erio}(\sum k_{OH,i}[X_i] + k_{OH}[dye])}{\sum k_{OH,i}[X_i]}$$

where $[OH^*_{ss}]$ is the OH^*_{ss} concentration in the absence of erioglaucine and $k_{OH,i}$ is the rate constant for OH* scavenging by some substance, X_i. If the concentrations and k_{OH} of the major scavengers, such as DOM, bicarbonate, etc., are known in addition to erioglaucine, then $[OH^*_{ss}]$ can be calculated from eq. 1. k's for reactions with OH* have been published for over 1700 compounds (but not erioglaucine; Buxton et al. 1988; Brezonik and Fulkerson-Brekken 1998; see also www.rcdc.nd.edu/compilations/Hydroxyl/OH.htm). If scavenger concentrations are not known, k can be used to compare samples provided that the initial erioglaucine concentrations are identical.

Although iron was used throughout this study as a reference solution, other substances such as nitrate and nitrite could also be used. Maximum values for first-order rate constants for production of OH* occurred at 322 nm with nitrate and at 355 nm with nitrite (Jankowski et al. 2000). Nitrate may be preferable to iron as a reference provided that there is sufficient UV below 330 nm because nitrate solutions are stable and because photoreactions involving nitrate are less sensitive to pH. Nitrite could be used in some applications. Iron and nitrite solutions should be mixed daily because these solutions are unstable, whereas nitrate is more convenient for extended field trips because nitrate solutions can be mixed before departure and kept for extended periods.

The fluorescent-type UVA and UVB lamps used in this study were very useful in the initial development stage of the erioglaucine assay. The incubator was inexpensive to build and permitted year-round research. The assay should,

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of course, prove useful under other types of UV lamps. However, future use of these light sources to examine natural samples is limited by the difficulty of transforming results to correspond to different light sources. To do so requires spectral response curves not for erioglaucine, which is insensitive to UV, but for each of the substances that photoproduce OH*. Future studies of natural samples should use either solar radiation or lamps that accurately mimic solar radiation as reference light sources to facilitate interlaboratory comparison of assay results. Experiments involving other types of lamps should, of course, conduct assays using those lamps.

Recommended protocol

Filter samples to remove coarse particulate matter (e.g., 1.2-μm membrane filter). Add erioglaucine to an initial absorbance of 0.60 at 620 nm (8.5 mg·L^{-1}). Use UV-transparent containers such as Teflon bottles, quartz vessels (preferred), or polyethylene bags with small sample volumes so that they are optically thin. Avoid Pyrex because of poor UVB transmission. Measure absorbance at 620 nm daily for up to 5 days in samples, in a reference solution (0.89 μM Fe (use 0.1 mM nitrate if there is sufficient UVB) at initial pH 4.5), and in a dye-only solution in deionized water. Incubate triplicates under UV (natural or artificial solar radiation recommended for natural samples). Measure irradiance if possible. Measure initial conditions: e.g., pH, nitrate, nitrite, DOM, total iron, dissolved inorganic carbon, and major anions to assist quantifying [OH^*_{ss}].

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Effects of episodic acidification on Atlantic salmon (*Salmo salar*) smolts

J.A. Magee, M. Obedzinski, S.D. McCormick, and J.F. Kocik

Abstract: The effect of episodic acidification on Atlantic salmon (*Salmo salar*) smolt physiology and survival in fresh water (FW) and seawater (SW) was investigated. Smolts were held in either ambient (control, pH 6.0–6.6), acidified (chronic, pH 4.4–6.1), or episodically acidified (episodic, pH reduction from control levels to pH ~5.2 for 48 h once weekly) river water for 31 days and then transferred to 34‰ SW. Smolts fed little while in acidified conditions and chronic smolts did not grow in length or weight. In FW, chronic smolts experienced increases in hematocrit and plasma potassium and reductions in plasma sodium and chloride. Upon transfer to SW, chronic and episodic smolts experienced reductions in hematocrit, increases in plasma sodium, chloride, and potassium levels, and suffered mortalities. Gill Na^+,K^+-ATPase and citrate synthase activities were reduced by exposure to acid. For most parameters, the effect of episodic acid exposure was less than that of chronic acidification. Exposure to acidic conditions, even when short in duration and followed by a 30-h recovery period in suitable water (pH 6.5), led to a 35% mortality of smolts upon transfer to SW. This study highlights the importance of measuring and assessing sublethal stresses in FW and their ultimate effects in marine ecosystems.

Résumé : Nous avons étudié les effets de l'acidification épisodique sur la physiologie des saumoneaux du saumon de l'Atlantique (*Salmo salar*) et sur leur survie en eaux douce (FW) et salée (SW). Les saumoneaux ont été gardés en eau de rivière pendant 31 jours, dans des conditions ambiantes (témoin, pH 6,0–6,6), d'acidification chronique (pH 4,4–6,1) ou d'acidification épisodique (réduction des niveaux témoins à pH ~5,2 pendant 48 h, une fois la semaine) et ensuite mis en eau de mer à 34 ‰. Dans les conditions d'acidification, les saumoneaux se nourrissent peu et ceux qui sont placées en acidification chronique ne croissent ni en longueur, ni en masse. En eau douce, les saumoneaux en acidification chronique subissent des augmentation de leur hématocrite et de leur potassium plasmatique et des réductions du sodium et des chlorures de leur plasma. Après un transfert en eau salée, les saumoneaux exposés aux conditions chroniques et épisodiques d'acidification subissent des réduction de leur hématocrite, des augmentations du sodium, des chlorures et du potassium de leur plasma et ils ont une mortalité accrue. Les activités de la Na^+,K^+-ATPase et de la citrate synthase sont réduites par l'exposition à l'acidité. Les effets d'une exposition périodique à l'acidité sont moins dommageables pour la plupart des paramètres que ceux d'une exposition chronique. L'exposition aux conditions acides, même de courte durée et suivie d'une période de récupération de 30 h en eau appropriée (pH 6,5), entraîne une mortalité de 35 % des saumoneaux lors de leur transfert en eau salée. Notre étude met en lumière l'importance de mesurer et d'évaluer les stress sublétaux en eau douce et leurs effets éventuels dans l'écosystème marin.

[Traduit par la Rédaction]

Introduction

Acidification of surface waters has led to the loss of fish species from lakes and rivers, with well-known losses of Atlantic salmon (*Salmo salar*) populations in southwestern Nova Scotia and Norway (Watt et al. 1983; Hesthagen and Hansen 1991). Severely acidified rivers have received much attention, but recent studies suggest that acidic episodes of short duration may have effects on Atlantic salmon populations in less acidified watersheds (Lacroix 1985; Buckler et al. 1995; Magee et al. 2001).

Upon exposure to acidic conditions in fresh water (FW), particularly with elevated inorganic aluminum, Atlantic salmon experience reduced feeding and growth (Saunders et al. 1983; Farmer et al. 1989), altered behavior (Pauwels 1990; Jagoe and Haines 1997), gill damage (Jagoe and Haines

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1997), and endocrine (Haya et al. 1985; Brown et al. 1990) and osmoregulatory disruption and death (Saunders et al. 1983; Lacroix and Townsend 1987; Staurnes et al. 1996). Even more severe is the inability of smolts to remain hypoosmotic in seawater (SW) after exposure to acidic conditions in FW (Farmer et al. 1989; Kroglund and Staurnes 1999; Kroglund et al. 2001*b*). This disruption of osmoregulatory capability may lead to reduced feeding and growth (Pauwels 1990; Damsgard and Arnesen 1998) and higher predation rates (Jarvi 1990; Handeland et al. 1996). Reduced growth has been implicated in lower probability of marine survival of Atlantic salmon smolts (Friedland et al. 1993).

In rivers and associated tributaries supporting Atlantic salmon in eastern Maine, episodes of low pH and high aluminum are more common than long-term acidic conditions (Haines et al. 1990). Episodes of increased acid and aluminum in low-calcium water have been shown to increase mortality and decrease feeding and growth in brook trout (*Salvelinus fontinalis*) fry even when episodes are moderate (decreased pH from 7.2 to 6.5) in severity (Cleveland et al. 1991). It is not known what effect episodes of increased acidity and aluminum have on long-term smolt physiology and survival. However, acute stress has been shown to reduce growth and alter endocrine function of Atlantic salmon parr (McCormick et al. 1998); both processes are important for smolting to proceed normally (Farmer et al. 1989; McCormick et al. 1995). Kroglund and Staurnes (1999) demonstrated that a concurrent decrease in pH (6.52 to 5.95) with a decrease in labile Al (LAl; 22 ± 16 to 15 ± 5 μg LAl·L^{-1}) for 24 h was sufficient to disrupt ionoregulation (plasma chloride levels) of smolts in FW. These smolts were able to recover to previous chloride levels after 3 days in limed (pH 6.28) water.

Data collected from several eastern Maine watersheds indicate that some tributaries and mainstem areas experience elevated acidity and aluminum that could impair ionoregulatory capabilities and survival of juvenile Atlantic salmon young-of-the-year, parr, and smolts (Haines et al. 1990).

Because episodes of increased acidity and aluminum associated with acid deposition are more common than chronically low pH in many river systems, we were interested in the effect of these episodes on smolt development and SW tolerance of Atlantic salmon. We hypothesized that episodes of increased acidity and aluminum would lead to osmoregulatory disruption in both FW and after transfer to SW. We tested this by examining the osmoregulatory capability of smolts exposed to periodic episodes of increased acidity and aluminum in FW and after their transfer to SW.

Materials and methods

Experimental animals

Smolts used in these experiments were 1-year-old Atlantic salmon smolts (F1 progeny of Penobscot River sea-run adults) reared at Green Lake National Fish Hatchery in Ellsworth, Maine. On 3 April 2000, 189 smolts (mean fork length ± standard error of the mean (SEM) = 172.2 ± 3.1 mm; mean weight ± SEM = 57.6 ± 3.3 g; n = 38) were taken to the Wild Salmon Resource Center in Columbia Falls, Maine. Sixty-three smolts were placed into each of three 1700-L square rearing tanks, which received ambient Pleasant River water (at 2.2 L·min^{-1}). This water first flowed into a 60-L header tank above each rearing tank. The residence time was approximately 13 h for the rearing tanks. The long residence time in the rearing tanks likely avoided the problem of unstable forms of aluminum (Kroglund and Staurnes 1999; Kroglund et al. 2001*a*). We used two air pumps with four air stones in each rearing tank to supply the smolts with abundant oxygen. The orientation of the incoming water created a slight, circular current in the tanks. A commercial pelleted food (50 g) was placed into each tank daily until 3 May.

Experimental design

Our goal was to keep the control tank at pH >6.2, the chronic tank at pH 5.0, and the episodic tank at pH 5.0 for 2 days and pH >6.2 for 5 days weekly. We slightly increased the total aluminum in the chronic and episodic tanks. On 8 April, we started the manipulation of pH and aluminum concentrations in the chronic and episodic tanks. We lowered the pH and increased the total aluminum by adding a stock solution (0.2% HCl and 0.981 g $AlCl_3 \cdot 6H_2O \cdot L^{-1}$) to the header tank at a rate of 2 mL·min^{-1} for the chronic and episodic experimental tanks. This generally lowered the pH by 0.75 units·day^{-1} and increased the total aluminum concentration by approximately 100 μg Al·L^{-1}. The control tank received unaltered river water for the duration of the experiment.

To assess the duration of osmoregulatory disruption, we sampled smolts during the third acid episode (sample 1) and 48 h after the episodic tank pH was allowed to increase to that of the control pH (a 48-h recovery period; sample 2). We sampled smolts after a 30-h recovery period from the fifth acid episode (sample 3). The physiological status at this time represents the status the smolts had before being SW-challenged. To assess the effect of prior FW acid exposure on hypoosmoregulatory ability in SW, we placed the remaining smolts into 34‰ SW (collected near Beals Island, Maine, and filtered to 5 μm) and sampled them after 24 h, 72 h, and 7 days.

Sampling and analytical methods

We randomly sampled 10 smolts from each treatment on 22 April (sample 1), 26 April (sample 2), and 8 May (sample 3) and sacrificed them by overdose of $NaHCO_3$-buffered tricaine methanosulfate. Length (to the nearest mm) and weight (nearest 0.1 g) were recorded. Six to 10 gill filaments were removed, placed into 100 μL ice-cold SEI buffer (150 mM sucrose, 10 mM ethylene diamine tetraacetic acid (EDTA), 50 mM imidazole, pH 7.3), and immediately frozen for determination of gill Na^+,K^+-ATPase and citrate synthase (CS) activity using the methods of McCormick (1993) and Leonard and McCormick (1999). Smolts were bled from the caudal vein and hematocrit was immediately read from centrifuged blood. The remaining blood was centrifuged at 3000 × g for 3 min, and the supernatant was removed and frozen at –20°C. Serum plasma sodium, potassium, and chloride concentrations were determined using an AVL 9810 electrolyte analyzer. We stopped the addition of acid and aluminum to the episodic tank on 5 May, and the pH slowly increased to 6.5 by 7 May. Thirty-six hours later (8 May), we conducted a SW challenge test (SWCT) using modified methods of Clarke (1982). We moved remaining smolts into 375 L of 5-μm-filtered 34‰ SW. We randomly sampled smolts after

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24 h, 72 h, and 7 days (on 9, 11, and 15 May) and analyzed the parameters described above. On 11 May, approximately 75% of the SW was replaced with SW of the same salinity collected and filtered that day.

We monitored temperature and pH hourly using automatic recording units (Hydrolab Datasonde 2, Hydrolab-Hach Co., Loveland, Colo., U.S.A.) and once daily with an Orion pH meter (Model 250 SA, Thermo Orion, Beverly, Mass., U.S.A.) and PerpHect electrode (Model 8256). The salinity of the SW was measured with a calibrated conductivity meter (YSI 600 XLM Sonde, YSI Inc., Yellow Springs, Ohio, U.S.A.). We analyzed cations, anions, dissolved organic carbon (DOC), acid-neutralizing capacity, closed-cell pH, and aluminum (total, organic, inorganic) of water in each tank on 5 May (during the fifth acid episode exposure) and 8 May (immediately before the SWCT) by standard methods (U.S. Environmental Protection Agency (USEPA) 1987). The sample was not filtered before passing it through the DOWEX column; therefore, this fraction contained both organically bound and particulate Al. We calculated the particulate Al (total (unfiltered) Al minus total dissolved Al) and subtracted this amount from the analyzed organic Al to obtain the "true" organic Al. We assumed the fraction of dissolved aluminum not bound to organics, termed LAl, to be the toxic form. LAl was calculated by subtracting the true organic from the inorganic fraction. The detection limit for all analyzed forms of aluminum was 10 $\mu g \cdot L^{-1}$. All water samples were taken and pH was measured near the tank outlet.

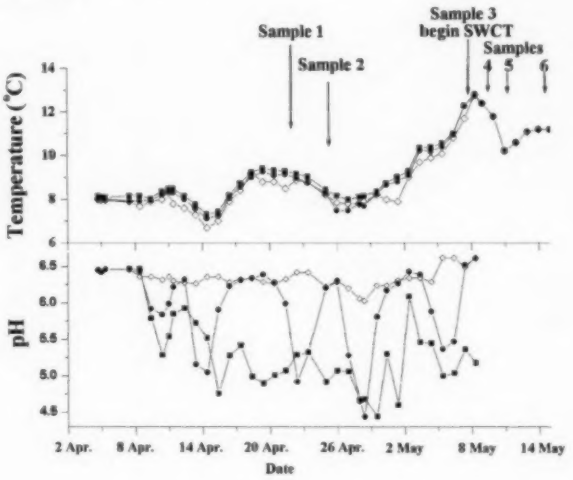
Statistical analyses

Data are presented as means ± SEM. A two-way analysis of variance (ANOVA) was conducted for each parameter using treatment and sample date as the independent variables. Differences over time were determined using Dunnett's test. We compared FW exposure means on 26 April and 8 May to 22 April and SW exposure means on 11 May and 15 May to 9 May. Differences between treatments within a sampling date were determined using Tukey's honestly significant difference test. Differences at $p < 0.05$ were considered significant.

Results

In FW, the temperature increased gradually from 8 to 13°C, and SW temperature varied between 10 and 13°C (Fig. 1). The pH in the control tank averaged 6.32 (range 6.2 to 6.5). Our planned additions of concentrated acid and aluminum solution and the variable river water composition led to designed and natural variability of pH in both the chronic and episodic tanks. Chronic tank pH averaged 5.25 from 10 April to 8 May. The pH ranged from 5.93 to 4.44 from 9 to 29 April and from 4.6 to 6.26 from 30 April to 8 May. The sharp increase in pH beginning on 1 May was due to an accidental decrease in the dosing rate on that day and was corrected on 2 May. Acidification episodes were initiated weekly in the episodic tank and effectively lowered pH as in the chronic tank. The average pH for all days during acid addition ($n = 15$) was 5.93 (includes those times when pH was increasing or decreasing). The average pH for days with no acid addition ($n = 21$) was 6.34. It was generally 1–2 days after the acid addition was terminated that the episodic treatment returned to the pH of the controls. The temperature and

Fig. 1. Temperature and pH of rearing tanks: control (open diamonds), chronic (solid squares), and episodic (solid circles) treatments. The temperature in all seawater (SW) rearing tanks was the same.



pH of the control tank was always within 1°C and 0.2 pH units of ambient Pleasant River water measured at Columbia Falls, Maine (data not shown), effectively mimicking the natural environment. The calculated LAl concentration was 23, 66, and 59 $\mu g\ LAl \cdot L^{-1}$ on 5 May for control, chronic, and episodic tanks, respectively. On 8 May, the calculated LAl concentration was 8, 67, and 15 $\mu g\ LAl \cdot L^{-1}$ for control, chronic, and episodic tanks, respectively. LAl on 8 May was low in the control and episodic tanks as a result of nearly complete complexation of Al with organics (Table 1). Calcium in all three treatments on these dates was 1.78–2.14 $mg \cdot L^{-1}$, and DOC was 6.8–7.3 $mg \cdot L^{-1}$.

Control smolts were active, fed eagerly, and used all areas of the tank, whereas chronic smolts fed little and often remained at the edges of the tank. During acid exposure, episodic smolts displayed behavior similar to that of chronic smolts but were active and fed eagerly when in ambient water. No smolts died while in FW; however, chronic and episodic smolts experienced mortalities in SW (Fig. 2). Only seven chronic smolts were alive after 72 h in SW, and these were sacrificed for analysis of physiological parameters. Control and episodic smolts grew slightly while in FW, whereas chronic smolts were significantly shorter and lighter at the end of FW exposure (Fig. 3). After 72 h in SW, chronic smolts were shorter and lighter than control and episodic smolts. After 7 days in SW, episodic smolts weighed 40% less than controls, despite being only 5% smaller in length. The fork length of survivors did not differ from that of smolts that died (t test, $p = 0.38$).

Exposure to acidified water had clear negative effects on gill Na^+,K^+-ATPase activity, with chronic smolts having the lowest activity on all sampling dates (Fig. 4). The gill Na^+,K^+-ATPase activity of episodic and chronic smolts did not increase from 22 April to 8 May and was lower than that of control smolts in both FW (8 May, after 5 weeks of pulse exposure) and after 24 h SW exposure. The Na^+,K^+-ATPase

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Table 1. Water quality parameters on 5 and 8 May and exposure groups.

Date collected	Treatment	Ca^{2+} ($mg \cdot L^{-1}$)	ANC ($\mu eq \cdot L^{-1}$)	TAl ($\mu g \cdot L^{-1}$)	DAl ($\mu g \cdot L^{-1}$)	PAl ($\mu g \cdot L^{-1}$)	OAl ($\mu g \cdot L^{-1}$)	TOAl ($\mu g \cdot L^{-1}$)	LAl ($\mu g \cdot L^{-1}$)	ClpH (pH units)	DOC ($mg \cdot L^{-1}$)
5 May	Ambient	1.85	92.4	148	109	39	125	86	23	6.18	7.3
	Episodic	1.78	2.5	257	216	41	198	157	59	4.97	7.1
	Chronic	1.81	–3.8	268	236	32	202	170	66	4.97	7.3
8 May	Ambient	2.01	118	144	103	41	136	95	8	6.36	7.1
	Episodic	2.14	117	184	107	77	169	92	15	6.25	6.8
	Chronic	2.09	9.8	300	228	72	233	161	67	5.25	6.8

Note: TAl, unfiltered aluminum (total dissolved and particulate); DAl, total dissolved aluminum; PAl, particulate aluminum (TAl minus DAl); OAl, analyzed organic aluminum (organic and particulate); TOAl, OAl minus PAl; LAl, labile aluminum (DAl minus TOAl); ClpH, closed cell pH; DOC, dissolved organic carbon. TAl, unfiltered aluminum (total dissolved and particulate); DAl, total dissolved aluminum; PAl, particulate aluminum (TAl minus DAl); OAl, analyzed organic aluminum (organic and particulate); TOAl, OAl minus PAl; LAl, labile aluminum (DAl minus TOAl); ClpH, closed cell pH; DOC, dissolved organic carbon.

Fig. 2. Cumulative mortality (%) of smolts in exposure groups: control (open diamonds), chronic (solid squares), and episodic (solid circles) treatments. No chronic smolts remained after 72 h in seawater (SW) because of mortality and removal for analysis of each physiological parameter.

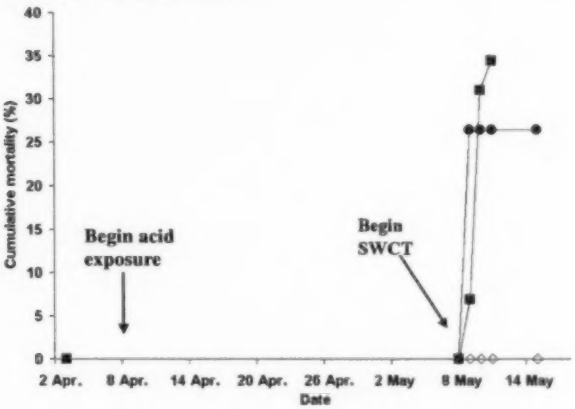
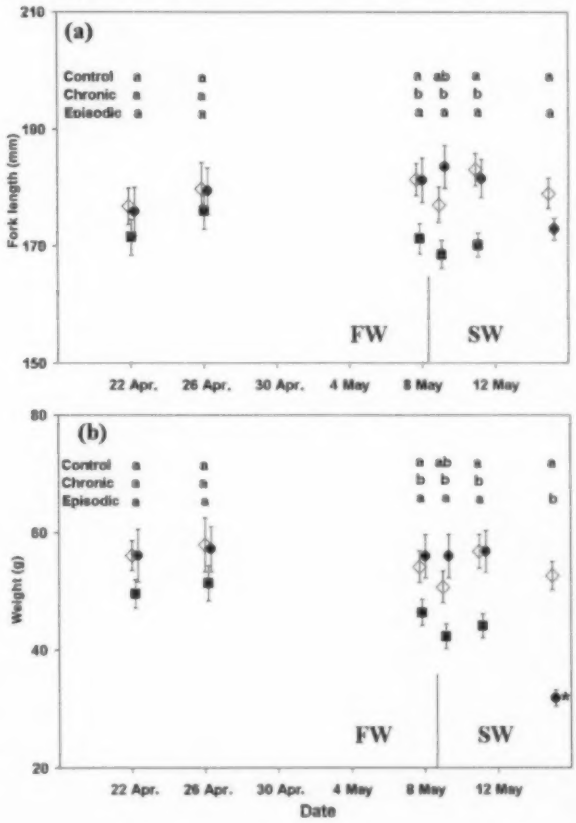


Fig. 3. (*a*) Fork length and (*b*) weight of exposure groups: control (open diamonds), chronic (solid squares), and episodic (solid circles) treatments. Asterisks (*) denote significant difference between 22 April and other freshwater (FW) dates and between 9 May and other seawater (SW) dates. Treatments with the same letter within a date are not significantly different. For all comparisons, $p < 0.05$ was used.



activity of surviving episodic smolts was similar to that of control smolts after 72 h in SW.

The effect of acid exposure on gill CS activity was similar to that on Na^+,K^+-ATPase activity, although not as pronounced (Fig. 4). Chronic and control smolts always had the lowest and highest activity, except after 72 h in SW when control smolts had the lowest and episodic smolts the highest.

Exposure to acidic water elicited similar effects on plasma sodium and chloride levels throughout the experiment (Fig. 5). During sample 1, chronic smolts had lower levels than the other treatments. Four days later (sample 2), plasma chloride of chronic smolts was lower than that of control but not that of episodic smolts. By this time, episodic smolts had been allowed to recover in ambient river water for 48 h, and sodium and chloride levels were nearly identical to those of control smolts. Chronic smolts had lower levels of sodium than those of the other treatments. During sample 3, when episodic smolts had recovered in control water for 30 h, the sodium and chloride levels of chronic smolts were lower than those of episodic smolts, whereas those of control smolts were intermediate. After 24 h SW exposure, chronic and episodic smolts had significantly elevated levels of both ions, and both groups suffered mortalities. Chronic smolts suffered additional mortality after 48 h in SW. After 72 h in SW, the surviving episodic smolts appeared to recover their ionoregulatory capabilities, whereas chronic smolts still had elevated plasma sodium and chloride. Episodic smolts had lower plasma sodium and chloride levels than controls after

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Fig. 4. Gill (*a*) Na^+,K^+-ATPase and (*b*) citrate synthase activity of exposure groups: control (open diamonds), chronic (solid squares), and episodic (solid circles) treatments. Asterisks (*) denote significant difference between 22 April and other freshwater (FW) dates and between 9 May and other seawater (SW) dates. Treatments with the same letter within a date are not significantly different. For all comparisons, $p < 0.05$ was used.

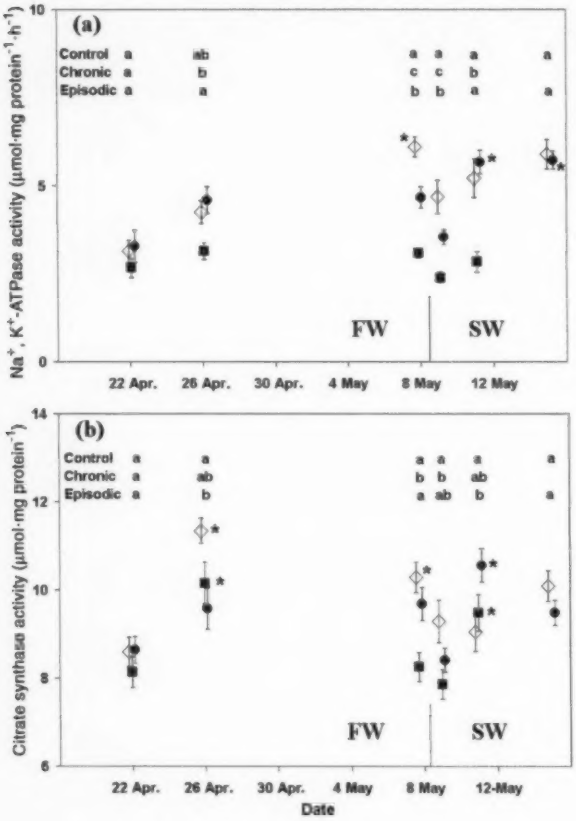
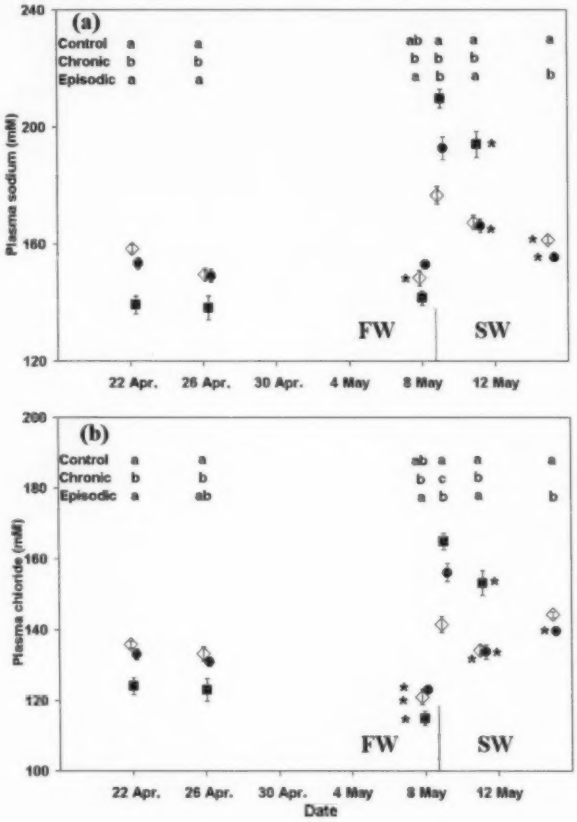


Fig. 5. Plasma (*a*) sodium and (*b*) chloride of exposure groups: control (open diamonds), chronic (solid squares), and episodic (solid circles) treatments. Asterisks (*) denote significant difference between 22 April and other freshwater (FW) dates and between 9 May and other seawater (SW) dates. Treatments with the same letter within a date are not significantly different. For all comparisons, $p < 0.05$ was used.



7 days in SW. Exposure to acidic water seemed to increase the plasma potassium levels of smolts, although not always significantly (Fig. 6). On most sampling dates, plasma potassium levels were lowest in control and highest in chronic smolts. Both acid-exposed groups had elevated plasma potassium levels after 72 h in SW, and plasma potassium was also elevated in the surviving episodic smolts after 7 days in SW. In general, hematocrit was inversely correlated with plasma sodium and chloride levels but was much less affected by acid exposure (Fig. 6).

Discussion

Generally, the physiological and behavioral responses to acid and aluminum stress in FW and subsequent SW exposure of control and chronic smolts in the present study were similar to those reported in other studies of Atlantic salmon (Kroglund and Staurnes 1999; Magee et al. 2001) and of brook trout in FW (Buckler et al. 1995). However, we found elevated plasma potassium, whereas others have documented reductions in or no effect on plasma potassium in response to acidified water (Lacroix and Townsend 1987; Booth et al. 1988). Smolts exposed to acid and aluminum lost plasma sodium and chloride in FW and were unable to remain hypoosmotic upon transfer to SW because of a reduction in Na^+,K^+-ATPase activity. This was likely the cause of mortality for the acid- and aluminum-exposed smolts. The present study differs from most in two important ways. First, we exposed smolts to discrete episodes of acidity. This is a more appropriate acid-exposure test relative to riverine ecosystems of Maine. This had a moderate physiological effect in FW, as inferred by plasma ion levels and hematocrit. Second, smolts were transferred to SW after they were allowed to recover in higher pH (~6.5) for 30 h. In other studies, smolts were placed into SW directly from acidified conditions. We allowed this recovery time to determine the effects of acid and aluminum on those smolts entering SW when the FW environment was more physiologically suitable. Our results indicate that prior acid and aluminum exposure significantly compromises salinity tolerance despite a 30-h recovery.

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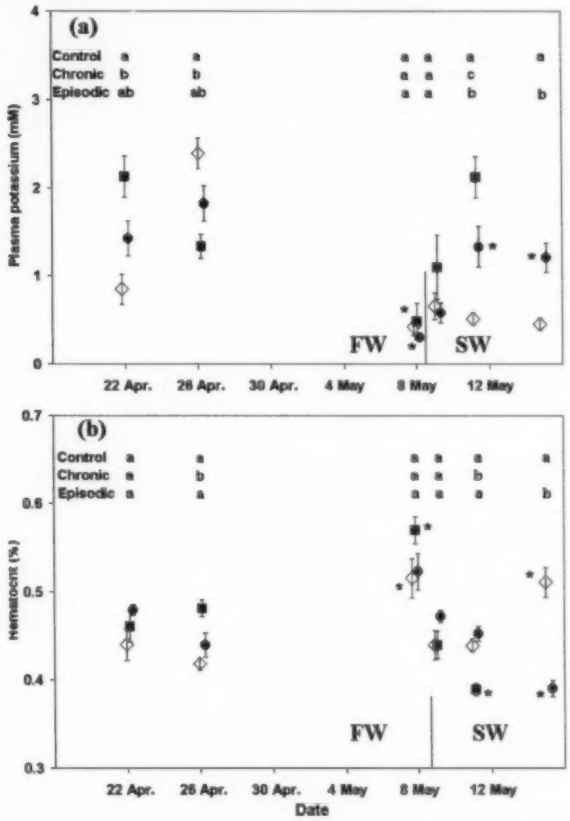
Fig. 6. Plasma (*a*) potassium and (*b*) hematocrit of exposure groups: control (open diamonds), chronic (solid squares), and episodic (solid circles) treatments. Asterisks (*) denote significant difference between 22 April and other freshwater (FW) dates and between 9 May and other seawater (SW) dates. Treatments with the same letter within a date are not significantly different. For all comparisons, $p < 0.05$ was used.



Osmotic stress has also been shown to affect the antipredatory behavior of Atlantic salmon smolts, leading to increased mortalities (Jarvi 1990; Handeland et al. 1996). In a telemetry study, Magee et al. (2001) found that a greater number of acid-exposed hatchery smolts returned upstream to FW shortly after migrating into SW of about 10‰ than did ambient-exposed (pH > 6.3) hatchery smolts. Additionally, those acid-exposed smolts that returned upstream remained in low-saline water for multiple tidal cycles, whereas the ambient-exposed smolts stayed in this section of the river for an average of only 12 h (usually one or two tidal cycles). Ambient-exposed (pH > 6.3) smolts migrated directly into SW without making upstream movements and remained in low-saline water for only a short time. Because estuaries represent an area of high Atlantic salmon predator abundance (Hvidsten and Lund 1988), minimizing time there should increase the survival rate of smolts. If smolts are suffering from osmotic stress (e.g., resulting from acidity) leading to altered migratory behavior, it is reasonable to expect smolt survival to be reduced.

Episodic smolts lost weight after 7 days in SW. This is likely due to a combination of dehydration and increased metabolic rate (basal and active metabolism may have been affected). Both of these may be directly linked to the reduced hypoosmoregulatory ability caused by acid exposure. Salmon juveniles transferred to SW outside of their normal period of smolt development when SW preparedness is high often develop into "stunts", having very low feeding and growth rates. Therefore, one may expect that long-term growth could be negatively affected by prior exposure to acid conditions. Friedland et al. (1993) correlated early marine growth to survival at sea for Atlantic salmon from the Connecticut River, U.S.A., and argued that slow-growing postsmolts do not survive in the marine environment. Crozier and Kennedy (1999) also concluded that marine growth influences marine survival of Atlantic salmon. Other studies have shown that continuous exposure to elevated acid and aluminum affects feeding behavior and leads to reductions in growth while in FW (Haya et al. 1985; Buckler et al. 1995). Based on our results, acidic episodes may similarly affect early marine survival by indirectly reducing early marine growth.

The time needed for recovery of acid-exposed smolts has been less well studied than other aspects of acid and aluminum toxicity. Kroglund and Staurnes (1999) determined that acid-exposed (pH 6.0 and 5.6) smolts were able to reestablish their plasma chloride levels within 3 days in pH 6.28 water, but they did not sample smolts until the end of the 3 days. Kroglund et al. (2001*b*) reported that smolt recovery (normal gill morphology, blood homeostasis, and SW tolerance) from exposure to acidic conditions was achieved within 9 days at pH 6.3. For brook trout fry in FW, swimming and feeding behavior were significantly altered even after a 48-h recovery period, but ionoregulatory parameters were not evaluated (Cleveland et al. 1991). Based on these studies, ionoregulatory recovery time seems to be on the order of at least 1–3 days provided that the water quality is good. However, episodic smolts were not able to recover their SW tolerance after 30 h because the 5-week episodic exposures led to a suppression of Na^+,K^+-ATPase. This demonstrates that ionoregulatory recovery in FW is not equivalent to complete physiological recovery. Recovery time of ionoregulatory ability in SW seems to be similar to recovery time in FW after acid exposure. Control and surviving episodic smolts in the present study were able to recover their ionoregulatory balance after 72 h in SW but not after 24 h. Handeland et al. (1996) reported that smolts suffering osmotic stress after transfer from FW to SW were able to stabilize their plasma chloride levels after 48 h.

Both chronic and episodic acid exposure led to a suppression in gill Na^+,K^+-ATPase and CS activities. These changes may have been causal to the reduced plasma ions in the chronic group in FW, as well as the reduced salinity tolerance seen in chronic and episodic groups. Current models of ion regulation in fish indicate that Na^+,K^+-ATPase is used for both ion uptake and salt secretion (Marshall and Bryson 1998). A reduced number of chloride cells as a result of acid exposure would explain reductions in Na^+,K^+-ATPase and CS activities as chloride cells have much higher amounts of these enzymes than other cell types in the gill. Most previous research suggests that acid and aluminum exposure results in an increase in the number of gill chloride cells (Reid

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1995; Jagoe and Haines 1997). If this occurred in the present study, then the reduced enzyme activities must have been due to reductions in the amount of these enzymes in chloride cells (or less likely, in other cell types of the gill). Just before the SW exposure, there was a significant decrease in gill Na^+/K^+ ATPase activity in the episodic group compared with the control, whereas no other change in FW physiology (plasma ions or hematocrit) was detected. After SW exposure, it was clear that the episodic group had decreased salinity tolerance. This indicates that changes in gill Na^+/K^+ ATPase activity are more sensitive than many other aspects of the animal's physiology in freshwater, providing a useful and sensitive indicator of subsequent performance in SW.

Results of the present study demonstrate that episodes of increased acidity and aluminum led to a suppression of gill Na^+,K^+-ATPase activity and subsequent reduction in hypoosmotic capability and survival in SW. The effect was less severe than for exposure to constant low pH (~5.2) for 5 weeks, and ionoregulatory disturbance was not manifest until after exposure to SW. These negative impacts on osmotic balance and growth may have substantial effects on the long-term growth and survival of smolts in the wild.

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Long-term changes in the trophic level of western Mediterranean fishery and aquaculture landings[1]

J.K. Pinnegar, N.V.C. Polunin, and F. Badalamenti

Abstract: We explored changes in western Mediterranean fishery and aquaculture landings using trophic level (TL) estimates derived from nitrogen stable isotope analysis combined with geographically detailed fishery data collated by the General Fisheries Council for the Mediterranean (GFCM). Our analyses confirmed earlier suggestions that there has been a significant decline in the mean trophic level of Mediterranean landings (by ~0.15 TL over 26 years). However, this decline is suggested to be almost entirely a result of increased landings of bivalve molluscs from mariculture and not due to changes in landings from capture fisheries. The mean trophic level of finfish landings has not changed significantly since 1973, although both fish and total landings have become significantly more diverse. Inspection of small pelagic fish landings revealed a marked decrease in the contribution played by anchovy and replacement of this species by sardine. Since 1981, cage culture of high trophic level species such as sea bass (*Dicentrarchus labrax*) and seabream (*Sparus aurata*) has become increasingly important, such that when clupeoid landings were excluded from the analyses, the mean trophic level of finfish landings was actually demonstrated to have increased over the past 26 years.

Résumé : L'estimation des niveaux trophiques (TL) par des analyses des ions stables d'azote combinée à des données sur les pêches commerciales comportant des informations géographiques détaillées et compilées par la Commission générale des pêches pour la Méditerranée (GFCM) nous a permis d'étudier les changements dans les débarquements des pêches commerciales et de l'aquaculture en Méditerranée occidentale. Nos analyses confirment les suggestions antérieures qui veulent qu'il y ait eu un déclin significatif du niveau trophique moyen des débarquements en Méditerranée (de ~0,15 TL en 26 ans). Cependant, ce déclin est dû, croyons-nous, presque entièrement à l'augmentation des débarquements de bivalves provenant de l'aquaculture et non à des changements dans les débarquements de poissons provenant de la pêche. Le niveau trophique moyen des débarquements de poissons n'a pas changé significativement depuis 1973, bien que les débarquements de poissons et les débarquements totaux soient devenus plus diversifiés. L'inspection des débarquements de petits poissons pélagiques révèle un déclin marqué de la contribution des anchois et leur remplacement par les sardines. Depuis 1981, la culture en cages d'espèces de haut niveau trophique, telles que le bar (*Dicentrarchus labrax*) et la dorade (*Sparus aurata*), est devenue de plus en plus importante, si bien que, si l'on exclut les débarquements de clupéidés des analyses, il apparaît, en effet, que le niveau tropique moyen des débarquements de poissons a augmenté au cours des 26 dernières années.

[Traduit par la Rédaction]

Introduction

Human exploitation of inshore marine resources dates back thousands of years in the Mediterranean, and most commercial fish stocks are considered to be greatly overexploited (Farrugio et al. 1993). The intensive exploitation of fish communities often leads to substantial reductions in the abundance of target species and changes in species composition overall. Large or slow-growing species with late maturity decline in abundance more rapidly than their smaller, faster-growing counterparts, and because large species generally feed at higher trophic levels, fishing is expected to reduce the mean trophic level of exploited communities (Pauly et al. 1998*a*).

Changes in the composition of landings often reflect changes in the structure of underlying fish communities (Pinnegar et al. 2002). Because landing data are collected for fisheries throughout the world, these data have been used to assess the large-scale and long-term effects of fishing on community trophic structure. Pauly et al. (1998*a*) used aggregated landing statistics from the United Nations Food and Agriculture Organisation (FAO), together with estimates of trophic

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levels for particular species derived from food-web models. For the Mediterranean and Black Sea (FAO area 37), Pauly et al. (1998*a*) demonstrated that the mean trophic level (TL) of landings declined significantly and steadily since the late 1950s, and this finding has prompted much interest (CIESM 2000) and debate (Caddy et al. 1998) with regard to the future sustainability of fishing in this region.

The decline in the mean trophic level of Mediterranean landings was purported to reflect a gradual transition from long-lived, high trophic level piscivorous bottom fish toward short-lived, low trophic level invertebrates and pelagic fish (Pauly et al. 1998*a*). These changes have also coincided with a gradual disappearance of artisanal gear (trammel nets, bogue gillnets, long lines, hand lines, pots, etc.) and a great expansion of semi-industrial trawling–seining techniques as well as aquaculture (Bas et al. 1985). There have been many assessments of the state of Mediterranean marine resources and long-term trends in catches and landings (e.g., Farrugio et al. 1993; Papaconstantinou and Farrugio 2000). Such studies have indicated that sizes of many demersal stocks have undergone a downward trend, particularly over the last 5 years, and one deduction from this has been that multispecies landings may now have exceeded a peak, especially in the western basin (Fiorentini et al. 1997; Papaconstantinou and Farrugio 2000). In contrast, the importance of aquaculture has continued to grow (Pedini 1996), having increased threefold from 85 000 tonnes (t) in 1985 to 251 000 t in 1995 and now accounting for around 16% of total production throughout the region.

Several concerns have been expressed about the approach used by Pauly et al. (1998*a*), and these have been discussed by Caddy et al. (1998), Caddy and Garibaldi (2000), and Pauly et al. (1998*b*). The principle concerns included the fact that aquacultural landings were not specifically accounted for, that increases in nutrient inputs to some seas and particularly the oligotrophic Mediterranean were not considered, while doubt was also cast upon the method of assigning trophic levels to individual species, and the validity of FAO landing data (Caddy et al. 1998).

The landing data used by Pauly et al. (1998*a*) covered the whole of the Mediterranean and Black seas. However, there are significant differences in the fisheries of the eastern and western Mediterranean Sea, with declining fisheries more common in the western subarea than in the east and Black Sea, where many stocks can be categorised as recovering or even rising (Papaconstantinou and Farrugio 2000). Large-scale geographic aggregation, as in the FAO data, makes it difficult to determine the species, environmental cues, or fleets responsible for the observed long-term changes in mean trophic level.

The trophic level estimates used by Pauly et al. (1998*a*) were obtained from mass–balance (Ecopath) models. However, at the time of publication, no model existed specifically for the Mediterranean and thus values were used for the same or closely related species from other, nearby seas. Many of the trophic levels obtained were derived from analysis of gut contents, which may provide only snapshots of diets in time and space and neglect certain dietary materials such as gelatinous plankton, microorganisms, and detritus, which can be an important constituent in the diet of some fish (Polunin and Pinnegar 2002). Gut-content analysis may be particularly problematic for predicting trophic levels of top predators that feed only intermittently and frequently regurgitate foods upon capture.

Stable isotopes of nitrogen have been widely used as an alternative and independent method of establishing trophic levels in aquatic organisms (e.g., Post 2002). The isotope method relies on the general observation that with every trophic level, there is bioaccumulation of the heavier isotope ^{15}N (Post 2002). Trophic level estimates resulting from stable isotope analysis (SIA) largely corroborate trophic level data derived from mass–balance modelling and (or) gut-content analysis (e.g., Pinnegar 2000). SIA offers several clear advantages because it integrates diet over a year or more in many fish species (Hesslein et al. 1993) and thus is much less subject to seasonal bias. Over the past 5 years, stable isotope data for many commercially important Mediterranean species have become available (Jennings et al. 1997; Pinnegar and Polunin 2000; Polunin et al. 2001), thus making it possible to re-examine the relationship proposed by Pauly et al. (1998*a*) using independently derived and geographically relevant trophic level estimates.

The objectives of the present study were (*i*) to examine long-term changes in the mean trophic level and diversity of fishery landings from the western Mediterranean subarea using stable isotope derived trophic level estimates and (*ii*) to examine whether such changes reflect the recent expansion of the aquacultural sector.

Methods

Stable isotope measurements

Samples of commercially important fish and invertebrates were obtained from four locations in the western Mediterranean (Fig. 1; Appendices A and B). For most species, stable isotope compositions have been reported elsewhere (e.g., Jennings et al. 1997; Pinnegar and Polunin 2000; Polunin et al. 2001); however, these data were supplemented with materials collected at Castellammare del Golfo (Sicily), the Bay of Calvi (Corsica), and western Mallorca (Appendices A and B). Additional top predators and pelagic species were obtained from local fish markets or directly from fishermen in Palma (Mallorca) and Castellammare (Sicily); these were assumed to have come from the surrounding waters. Species of mollusc were obtained from the market in Castellammare del Golfo but are known to have originated in the Adriatic (Appendix B).

Values reported by Jennings et al. (1997) were recalibrated in accordance with a correction factor described by Pinnegar (2000). In each case, white muscle samples were taken from fish, adductor muscle from bivalves, mantle tissue from cephalopods, and tail muscle from large crustaceans, whereas small crustaceans were analysed whole. The conventional δ (delta) notation was used throughout to express stable isotope ratios, and these were reported relative to an international standard (atmospheric nitrogen):

$$(1) \qquad \delta^{15}N = [(R_{sample}/R_{standard}) - 1] \times 1000$$

where R is the ratio of ^{15}N to ^{14}N.

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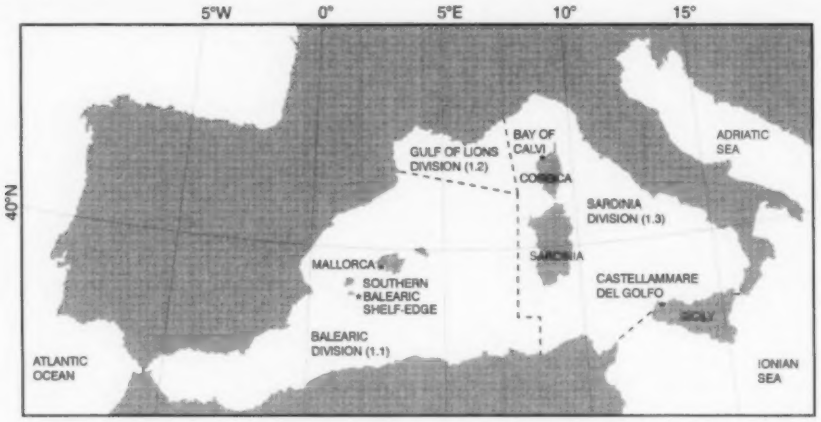
Fig. 1. General Fisheries Council for the Mediterranean (GFCM) statistical divisions of the western Mediterranean and the four main sample collection sites (★).



Trophic level estimates

Stable isotope estimates of trophic level were calculated assuming a constant per-trophic-level fractionation of 3.4‰. Post (2002) demonstrated that this fractionation pattern is remarkably consistent, irrespective of whether the animal concerned is a herbivore, carnivore, or detritivore. As reference material, values for zooplankton from each of the Mediterranean sites (mainly copepods) were utilised whereby

$$(2) \qquad TL_{N_i} = [(\delta^{15}N_i - \delta^{15}N_{ref})/3.4] + 2$$

TL_{N_i} is the trophic level of species i, $\delta^{15}N_i$ is the mean $\delta^{15}N$ of species i, and $\delta^{15}N_{ref}$ is the mean $\delta^{15}N$ of the zooplankton, which were assumed to be herbivorous–detritivorous and feeding at trophic level 2. The mean $\delta^{15}N$ of the zooplankton "baseline" materials from each study site ranged widely. The value for the Bay of Calvi was 3.43 ± 0.22‰ (standard error (SE); communities sampled by Pinnegar and Polunin 2000) and 3.50 ± 0.11‰ (communities sampled by Lepoint et al. 2000), for western Mallorca, 3.94 ± 0.08‰, and for Castellammare del Golfo, 3.69 ± 0.23‰, and the value for the southern Balearic Islands (deep-sea communities) varied depending on depth (5.25 ± 0.22‰ at 200–800 m, 5.54 ± 0.09‰ at 800–1425 m, and 6.57 ± 0.16‰ at 1425–1800 m). For the molluscs that were derived from the upper Adriatic Sea, a locally measured baseline of *Spisula subtruncata* (8.4 ± 0.06‰), which is known to feed mainly on phytoplankton (Camusso et al. 1999), was used.

Trophic level estimates obtained using stable isotopes of nitrogen were compared with trophic level estimates recently reported by Stergiou and Karpouzi (2002) based on gut-content analyses.

Fishery landing data

Nominal landing data from capture fisheries and aquaculture (in tonnes live weight) for the Mediterranean and Black seas (FAO area 37) are assembled on an annual basis by the General Fisheries Council for the Mediterranean (GFCM). These data are in turn used as the basis for the annual FAO assessment, but unlike the geographically aggregated FAO data, GFCM statistics are available for individual subareas and divisions. In the present paper, only data for the western subarea of the Mediterranean, which includes the Balearic, Gulf of Lions, and Sardinia divisions (Fig. 1), were analysed. Data spanning 1972–1998 were downloaded from the web site of the FAO (www.fao.org/fi/) and covered all harvest by commercial, artisanal, and subsistence fisheries as well as aquaculture. A second data set covering only landings from capture fisheries and excluding all aquaculture production was downloaded when this became available. Landings were aggregated by species, irrespective of country or division, and species not harvested for consumption (e.g., sponges and red coral) were excluded. No data concerning tuna and billfishes (swordfish, sailfish, and marlin) were available specifically for the western Mediterranean subarea, and thus these species were also excluded.

Statistical analysis

Mean trophic level estimates for each year of the time series were calculated as

$$(3) \qquad \text{Mean trophic level} = \sum_{i=1}^{n}\left(TL_{N_i}\left(\frac{Y_i}{\sum Y}\right)\right)$$

where Y_i is the total landings of species i (in tonnes), ΣY is the sum of landings for all species, and TL_{N_i} is the trophic level estimate for species i derived from stable isotope analyses. To test for significant long-term trends in time series data, nonparametric Mann–Kendall tests (Z) were performed. The Mann–Kendall test is particularly useful because data need not conform to any particular distribution (Gilbert 1987).

Spearman's rank correlation (r_S) was used to establish whether there was a significant relationship between mean trophic level and total landings (in tonnes). Shannon–Wiener diversity (H') of the landings was calculated for each year of the time series. Data were log-transformed where it was deemed necessary to achieve homogeneity of variances (f_{max} test), and differences were judged significant when $P < 0.05$. For some analyses, species were grouped into ISSCAAP (International Standard Statistical Classification of Aquatic Animals and Plants) categories.

A coefficient of variation (CV) was calculated for each estimate of trophic level (Appendix A) using the "delta method"

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(Seber 1982). This took into account variances associated with the $\delta^{15}N$ of the consumer, with the $\delta^{15}N$ of the baseline material, and with the per-trophic-level fractionation factor (assumed to be 3.4 ± 0.13‰ according to Post (2002)).

Results

Stable isotope and trophic level estimates

Stable nitrogen isotope compositions were gathered for 88 species of marine fishes (Appendix A) and 34 species of commercially important invertebrates (Appendix B).

When reexpressed as trophic level relative to a zooplankton baseline, most fishes appeared to occupy a trophic level of between 3 and 4 (with a mean of 3.75) and ranged from 2.31 (*Cyclothone braueri*) to 4.58 (*Torpedo torpedo*). Estimates for CV were generally around 0.3, and this was greatly influenced by the variance associated with the per-trophic-level fractionation factor (taken from Post 2002). There was a strong correlation between trophic level estimates obtained from nitrogen stable isotopes and those provided by Stergiou and Kapouzi (2002) based on gut-content analyses ($r = 0.48$, $p = 0.0001$; Fig. 2).

Trophic level estimates for invertebrates were generally lower than those for fish; however, some cephalopods and large decapod crustaceans exhibited relatively high values (Appendix B). The mean TL was 3.51 for cephalopods, 2.25 for bivalves, 3.13 for decapod crustaceans, and 2.36 for other invertebrates (echinoderms and tunicates).

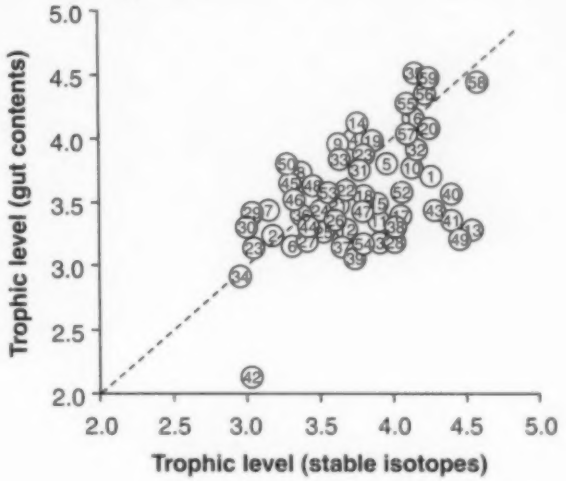
Diversity and total landings

Total fishery and aquaculture landings increased from 1972 to 1998 (Mann–Kendall $Z = 4.003$, $P = 0.0004$), although they seem to have reached a peak in 1994 at 460 860 t and thereafter subsequently declined to 379 541 t (Fig. 3*a*). Capture fishery landings (excluding aquaculture) exhibited similar patterns, although they increased less markedly ($Z = 1.793$, $P = 0.054$). Over the 26-year period between 1972 and 1998, there was also a significant increase in the H' of landings ($Z = 3.127$, $P = 0.002$; Fig. 3*b*). By contrast, the diversity of finfishes did not show any clear or significant trends ($Z = 0.250$, $P = 0.803$), varying widely between 2.0 and 2.4. Particularly low indices were estimated for 1988 (2.00) and 1994 (2.03), years in which catches were dominated by sardine. When all clupeoids (ISSCAAP group 35) were excluded from the analysis (Fig. 3*c*), the result was a gradual and highly significant increase in finfish (mostly demersal species) diversity ($Z = 4.268$, $P < 0.0001$).

Changes in mean trophic level and catch composition

The mean trophic level of all landings declined significantly (Mann–Kendall $Z = -3.725$, $P < 0.0004$) over the course of the 26-year time series (Fig. 4*a*), from around 3.40 in 1972 to 3.25 in 1998, although most of the change occurred between 1988 and 1989. There was no significant correlation between mean trophic level and total landings ($r_S = 0.352$, $P > 0.05$), although there were substantial changes in catch composition (Fig. 4*b*). The proportion of the landings represented by fish declined significantly from 82.6% in 1972 to 74.3% in 1998 ($Z = -4.000$, $P < 0.0004$). On the other hand, the proportion represented by bivalve molluscs increased from 6.72 to 17.92% ($Z = -4.003$, $P < 0.0004$).

Fig. 2. Trophic level of 59 species of Mediterranean fish, estimated using stable isotopes of nitrogen and gut-content analyses (from Stergiou and Karpouzi 2002). Species identifiers (numbers) are given in Appendix A.



This expansion was largely attributable to the increased harvesting and aquacultural production of low trophic level, bivalve molluscs such as *Crassostrea gigas* and *Mytilus galloprovincialis* (Fig. 4*c*). When landings of *C. gigas* (TL 2.36) and *M. galloprovincialis* (TL 2.24) were maintained at their 1984 levels (for the period 1984–1998), the apparent overall trend in mean trophic level became insignificant ($Z = 0.042$, $P = 0.968$). When all aquaculture landing data were excluded, the decline in mean trophic level (Fig. 4*d*), although still significant ($Z = -3.877$, $P = 0.006$), was much less marked. Trophic level declined by only 0.07 over the entire 26 years.

Changes in finfish landings

The mean trophic level of finfish landings varied greatly between 1972 and 1998 and exhibited no significant trend over the course of the time series ($Z = 0.208$, $P = 0.834$). By contrast, finfish landings (in tonnes) increased significantly over the 26 years ($Z = 2.126$, $P = 0.033$), reaching a peak of 362 890 t in 1994 but declining thereafter to 281 215 t in 1998 (Fig. 5*a*). An analysis of catch composition in terms of standard ISSCAAP groupings (Fig. 5*b*) did not reveal any major changes between 1972 and 1998, although the proportion represented by clupeoids (sardines and anchovies) increased ($Z = 3.002$, $P = 0.003$), whereas the proportion represented by "jacks, horse-mackerels, and grey mullets" (ISSCAAP group 34) contracted slightly ($Z = -3.794$, $P < 0.0004$), as did the proportion represented by gadoids ($Z = -2.293$, $P = 0.022$).

Within the clupeoids (ISSCAAP group 35), there was a significant reduction ($Z = -3.544$, $P < 0.0004$) in the importance of anchovy (*Engraulis encrasicholus*) between 1981 and 1986 and a replacement of this species with sardine (*Sardina pilchardis*) and gilt sardine (*Sardinella aurita*), larger species that generally feed at a higher trophic level (Fig. 5*c*). This change in species abundances corresponded

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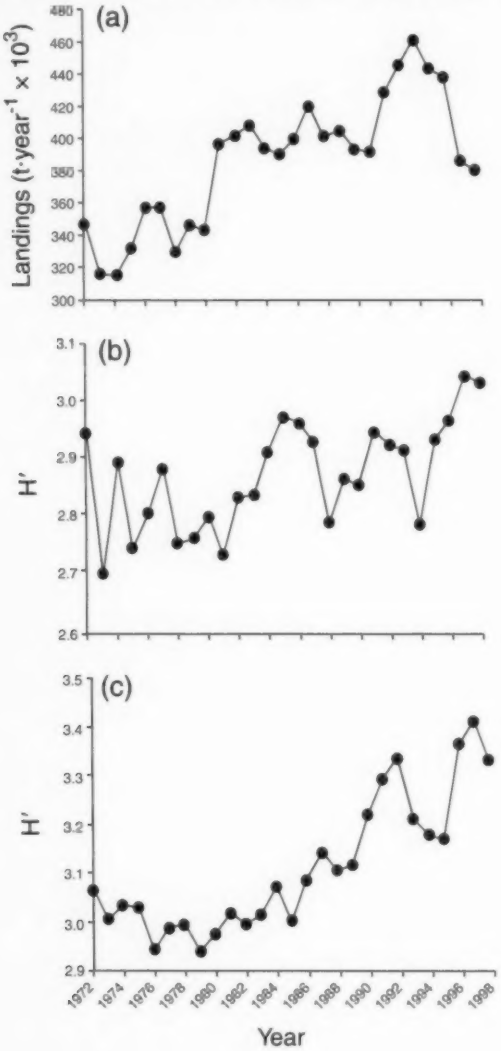
Fig. 3. Patterns of changing (*a*) total landings and Shannon–Wiener diversity (H') of (*b*) total landings and (*c*) finfish landings excluding all clupeoids (International Standard Statistical Classification of Aquatic Animals and Plants (ISSCAAP) group 35).



closely with the period of observed increase in H' (Fig. 3*c*). Removal of clupeoids from the analysis revealed a marginally significant (Z = 1.918, P = 0.054) increase in the mean trophic level of capture fishery and aquaculture landings.

Within the "sea basses, redfishes, and congers" (ISSCAAP group 33), several important trends were notable. Over the course of the 26-year time series, landings of gilthead seabream (*Sparus aurata*) and sea bass (*Dicentrarchus labrax*), both high trophic level species, increased markedly (Z = 5.754, $P < 0.0004$), largely as a consequence of an expansion of cage aquaculture on these species (Fig. 5*d*). By contrast, landings of the red mullet (*Mullus surmuletus* and *Mullus barbatus*) declined significantly over this period (Z = –2.960, P = 0.003). The expansion of *S. aurata* and *D. labrax* landings closely mirrored the observed period of increase in the diversity of finfish landings (Fig. 3*c*). The contribution of aquaculture to total French, Italian, and Spanish landings of *S. aurata* and *D. labrax* rose from 31.4 and 21.2%, respectively, in 1990 to 83.7 and 65.5%, respectively, in 1998. No significant change was detected in the mean trophic level of finfish landings (Z = 0.208, P = 0.779) once aquaculture landings had been excluded, even when all clupeoid landings were also eliminated (Z = 1.418, P = 0.156).

Discussion

Trends in trophic level and diversity

The decline in the mean trophic level of landings that we observed for the western Mediterranean (~0.15 TL over 26 years) is of similar magnitude to that given by Pauly et al. (1998*a*; ~0.11 TL over 26 years) for the Mediterranean and Black seas as a whole.

Coincident with the observed decline in mean trophic level has been an increase in H', both overall and for finfishes (excluding clupeoids). This reflects diversification and (or) substitution in the species being targeted (marketed), as might be expected where the supply of the preferred target species has begun to dwindle (Pinnegar et al. 2002). Because it is known that there has been some improvement in the discrimination of species since the early years of the time series, we cannot exclude the possibility that the apparent increase in diversity may be due to a degree of error in reporting, with fewer species now being included in undifferentiated categories (Fiorentini et al. 1997). However, most of the "new" species recently reported in GFCM data represent only a minor proportion of the total biomass and would thus impact Shannon–Wiener diversity only very weakly.

Limitations and assumptions of the analyses

There are several potential limitations of our analyses, some of which were discussed by Caddy et al. (1998) and stem from problems in the FAO or GFCM data. However, others include the known problem that Mediterranean landings may have been grossly underestimated, because in several GFCM countries, statistics are obtained from fishermen for tax collection purposes (Papaconstantinou and Farrugio 2000). Additional limitations of our analyses stem from our estimates of trophic level.

The feeding habits of fishes are commonly size-dependent such that as an animal grows, its diet and thus the trophic level at which it feeds will tend to change. Clearly the concept of assigning a single trophic level to a species, i.e., the procedure adopted here and by Pauly et al. (1998*a*), may be problematic. However, because most species feed at a lower trophic level when they are smaller and fishing pressure usually reduces the mean size of the fish in the community, the effect will almost always be conservative. If taken into account, changes in size composition might actually enhance the apparent "fishing down of marine food webs" effect (Pauly et al. 1998*b*). Indeed, Jennings et al. (2002) used body size – trophic level relationships for North Sea fishes combined with species abundance data collected between

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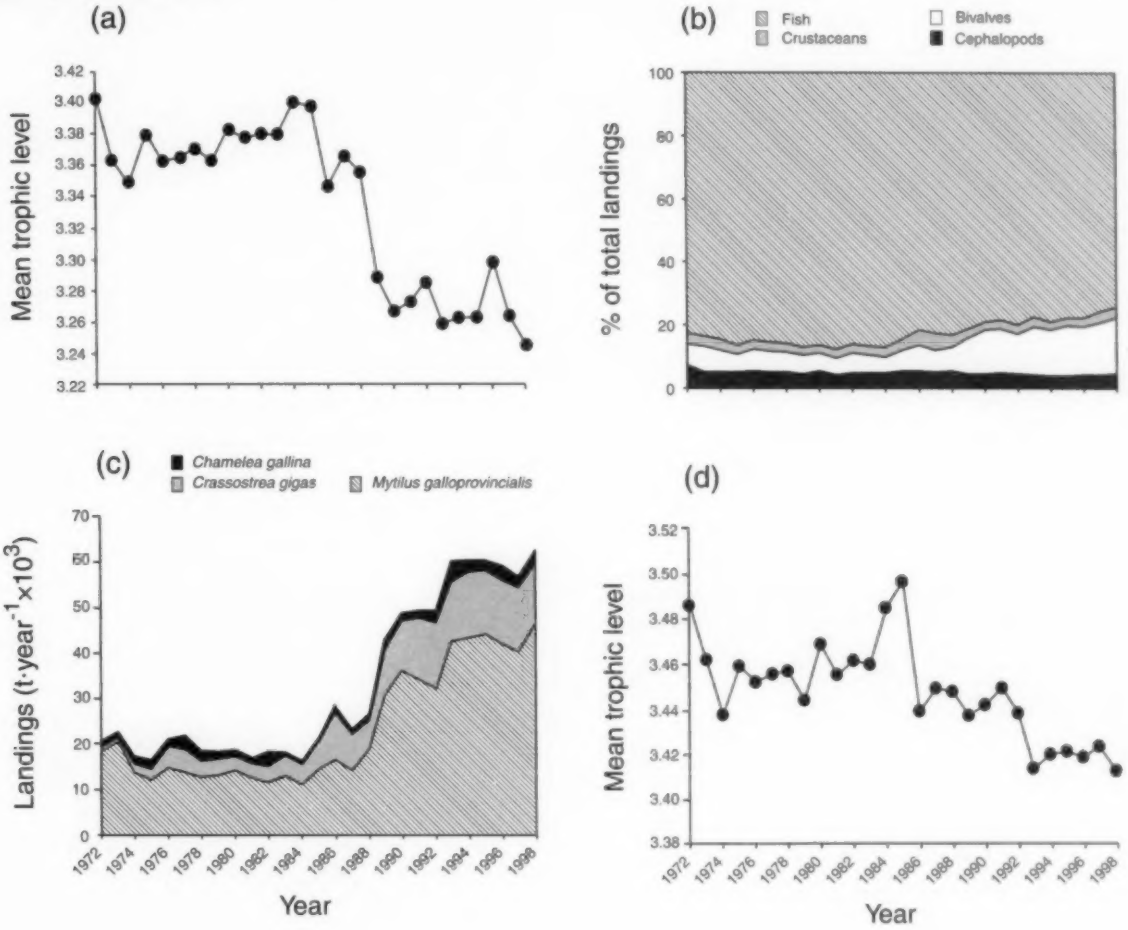
Fig. 4. Patterns of changing (*a*) mean trophic level in General Fisheries Council for the Mediterranean (GFCM) capture fishery and aquaculture landings, (*b*) composition of GFCM landings, (*c*) bivalve mollusc landings, and (*d*) mean trophic level of capture-fishery (excluding aquaculture) data.



1926 and 2000 and found a slow but progressive decline in the mean TL of the community. This decline was significant only when changes in size structure were accounted for and could not be discerned using fixed trophic level estimates for species. Ideally, it would be possible to use trophic level at length data for all species in the present analysis, and some stable isotope derived data are available for commercially important Mediterranean species (Badalamenti et al. 2002). However, these data are by no means sufficient to allow the detailed analyses demonstrated by Jennings et al. (2002).

Although trophic level estimates obtained from stable isotope analyses largely corroborate trophic level data derived from mass-balance modelling and gut contents (Pinnegar 2000), there are sometimes clear discrepancies in the estimates obtained from the two approaches (Badalamenti et al. 2000). In the present study, estimates obtained for several species of soft-bottom fish (e.g., *M. barbatus*, *Syphurus ligulatus*, *Solea impar*, and *Solea solea*) and the large sparid fish (e.g., *Pagellus acarne*, *Pagellus erythrinus*, and *S. aurata*) were higher than might generally have been expected for species feeding mainly on benthic invertebrates. Soft-bottom ecosystems may be very complex such that some benthic invertebrates may feed several trophic levels higher than others in the same system. Many polychaete worm species, for example, feed almost exclusively on other polychaetes and thus feed at a relatively high trophic level. Some soft-bottom fish are known to particularly select these carnivorous polychaetes (Badalamenti et al. 2000), and such subtleties are rarely appreciated from gut-content studies (e.g., those in Stergiou and Karpouzi 2002) or incorporated in ecosystem models (e.g., those of Pauly et al. 1998*a*). The reasons why trophic level estimates differed markedly for the herbivorous species *Sarpa salpa* (species No. 42) are described elsewhere (Pinnegar and Polunin 2000; Polunin and Pinnegar 2002).

In assigning a single trophic level to each species, we (but also Pauly et al. 1998*a*) have ignored the possibility that diet

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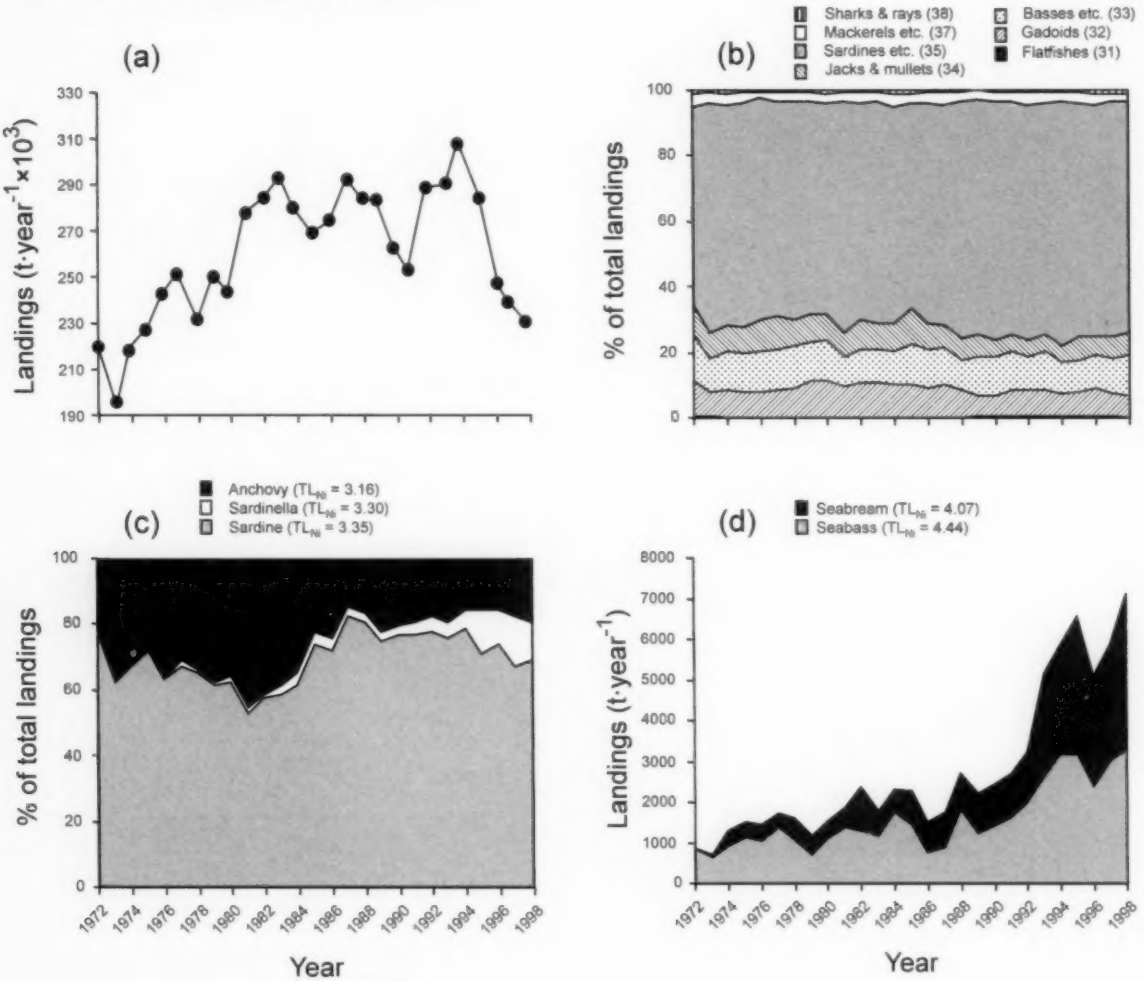
Fig. 5. Patterns of changing (*a*) finfish total landings (aquaculture and capture fisheries), (*b*) composition of finfish landings in terms of International Standard Statistical Classification of Aquatic Animals and Plants (ISSCAAP) groupings (group number in parentheses), (*c*) clupeoid landings (trophic level (TL_{Ni}) in parentheses), and (*d*) sea bass (*Dicentrarchus labrax*) and gilthead seabream (*Sparus aurata*) landings (trophic level (TL_{Ni}) in parentheses).



composition may have actually changed over the course of the 26-year time series. Stable isotopes analyses have demonstrated elsewhere that the diet of marine fishes has changed significantly over the past century in response to changes in the abundance of their main prey (e.g., Wainright et al. 1993). Without sufficient archived materials being available in museums and fishery institutions, it would be very difficult to test this possibility in the Mediterranean.

One final limitation of our trophic level data concerns the assumption that zooplankton (which were used as the baseline) always occupy trophic level 2. Clearly, zooplankton samples consist of a mixture of herbivorous, detritivorous, and carnivorous animals, thus their composition and also their isotopic signature may vary markedly throughout the year (Pinnegar 2000). To avoid such problems, some authors (e.g., Post 2002) have chosen to use slow-growing mollusc species as the trophic level baseline. Such materials were not collected by each author included in the present synthesis (Jennings et al. 1997; Pinnegar and Polunin 2000; Polunin et al. 2001) and at each of the four Mediterranean sites. Zooplankton were the only basal materials common to each study, and although we accept the limitations of using such data, we have attempted to account for potential error in our trophic level estimates by calculating an overall CV. For some sites (e.g., the Bay of Calvi, Corsica), it is known that the zooplankton samples used were dominated by herbivorous copepods such as *Clausocalanus arcuicornis* (Pinnegar 2000). In addition Stergiou and Karpouzi's (2002) estimates of trophic levels based on gut-content data also assumed a trophic level of 2 for planktonic copepods.

The rise of aquaculture

In their original assessment of trophic level decline in global fishery landings, Pauly et al. (1998*a*) did not specifi-

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cally account for the role played by expanding aquacultural production (Caddy et al. (1998) and response in Pauly et al. (1998*b*)). Aquaculture contributes a much higher share (~16%) of total production in the Mediterranean than is the case anywhere else in the northeast Atlantic (Symes 1999), and a dramatic increase in the production of low trophic level bivalve molluscs (TL ~2.6) would be expected to enhance the apparent fishing down of marine food webs (Caddy et al. 1998). Indeed, when aquaculture landings were excluded from our analyses, the apparent decline in the mean trophic level of Mediterranean landings over the 26-year time series was greatly weakened. Thus it would seem that the documented overall decline in mean trophic level of Mediterranean landings is almost entirely due to the rise in importance of aquaculture. Of the three western Mediterranean statistical divisions, bivalve production increased most markedly in the Sardinia division, especially through the expansion of Italian and French operations (Pedini 1996). Red tides have apparently been a major problem for mollusc production in Spain (Pedini 1996).

Initially, most finfish culture in the Mediterranean focussed on grey-mullets (Pedini 1996), species that naturally feed at relatively low trophic levels (e.g., *Liza ramada*, TL 3.24). However, sea bass and seabream, which have dominated in recent years, are high trophic level species, and Pauly et al. (1998*b*) suggested that the culture of high trophic level finfishes may in fact counter the fishing down of marine food webs apparent from landings data. When sardine and (or) all clupeoids were excluded from the analyses, a slight increase in the mean trophic level of finfish landings became apparent. This, together with a pattern of increasing finfish diversity, closely mirrored the period of expansion in landings of cultured sea bass and seabream. No increasing pattern in mean trophic level was detectable when aquaculture landings were excluded.

Changes in capture fisheries

Stergiou (1999) has suggested that many Mediterranean top predators (e.g., *Coryphaena hippurus*) may have been all but "fished out" in antiquity, as even very small amounts of fishing pressure can quickly deplete such species. Early fisheries, as depicted in Roman, Greek, or Egyptian frescos, tended to involve highly selective gears, and consequently, it is possible that many fishing-induced changes occurred in Mediterranean fish assemblages long before our 26-year time series or even the 50-year time series used by Pauly et al. (1998*a*). Desse and Desse-Berset (1993) demonstrated that inshore systems in Cyprus have been impacted for millennia and that large specimens of certain species, notably seabreams (Sparidae) and groupers (Serranidae), are now much rarer than they were during the Neolithic (~6000 BC). By contrast, Caddy and Garibaldi (2000) suggested that stocks of several offshore and pelagic piscivores (e.g., swordfish, *Xiphias gladias*, and bluefin tuna, *Thunnus thynnus*) might have actually increased in the Mediterranean over recent years in response to a greater abundance of their prey, small pelagic fish species (Caddy and Garibaldi 2000). Tuna and billfishes were not included in the present analyses for the western Mediterranean.

The increased importance of small pelagic species in Mediterranean landings may in part be a response to scarcity of more desirable target species (i.e., a switch in fishery preferences) or due to environmental change. However, it is also possible that this was related to technical innovation and the development of new gears. The technological revolution of the 1950s and 1960s allowed large-scale, midwater trawling and purse-seining by industrial fleets for the first time. This, in turn, has greatly increased the vulnerability of small pelagic stocks worldwide over the last few decades (Caddy and Garibaldi 2000).

Environmental influences

The Mediterranean was already considered fully exploited in the 1970s (Caddy and Garibaldi 2000), and many demersal stocks in the western basin were known to be in decline or close to their maximum sustainable yield (MSY; Papaconstantinou and Farrugio 2000). Therefore, it might seem surprising that total landings increased from 1972 to 1994. Landings per unit shelf area in the western subarea of the Mediterranean increased significantly in the 1970s and 1980s, and the contribution of anthropogenic nutrients has been proposed as a major factor here (Caddy et al. 1995). Pelagic resources seem to have particularly benefited from the eutrophication of the western Mediterranean, and the expansion in clupeoid landings and bivalve mariculture that we document in this study may have been related to this. Demersal landings have increased less markedly, and it has been proposed that eutrophication may eventually render benthic habitats less suitable for demersal predatory and piscivorous species, mainly because of reduced oxygen levels in bottom waters, thus resulting in the establishment of a fish community dominated by small pelagic species (De Leiva Moreno et al. 2000).

Alternation between high landings of anchovy and sardine has been reported for many years throughout the western Mediterranean (e.g., Bas et al. 1985). These changes seem less the result of fishing pressure and more a consequence of ecological factors, such as variations in the composition of phytoplankton on which the larvae feed.

Long-term climate change might also greatly affect the composition of fish communities. Over the past 20–30 years, a significant increase has been observed in the average temperature of western Mediterranean waters (Bethoux et al. 1990). Many "thermophilic" species (including *Sardinella aurita*) have become increasingly abundant (Francour et al. 1994). Changes in the composition of ichthyofauna have had a considerable impact on local fishing industries (Francour et al. 1994).

In conclusion, our analyses have confirmed the suggestion of Pauly et al. (1998*a*) that there has been a significant decline in the mean trophic level of Mediterranean landings. However, it would appear that this decline may be almost entirely the result of increased landings of bivalve molluscs from mariculture and not due to changes in capture fishery landings; consequently, we can say very little about the future sustainability of fisheries in the region or the potential for trophic collapse.

There is some evidence for changes in the species of finfish being landed and evidence that landings (both for finfish and overall) have become more diverse in recent years. Furthermore, the mean trophic level of finfishes (excluding clupeoids) may have actually increased over the past 26

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years, reflecting increased cage culture for sea bass and seabream. In other areas of the North Atlantic, aquacultural production remains relatively small scale (e.g., the Celtic and North seas), and observed trends in mean trophic level of landings are undoubtedly the result of changes in capture fishery landings (e.g., Pinnegar et al. 2002; Jennings et al. 2002).

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(Appendix A next page.)

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Appendix A

Table A1. Database of $\delta^{15}N$ data, trophic level, and mean size (total length) for 88 Mediterranean fishes.

Order and species	ISSCAAP code	$\delta^{15}N$ (±SE)	Trophic level	CV	*n*	Mean size (cm ± SE)	Location	Reference	Figure 2 ID
Anguilliformes									
Conger conger (deep)	33	12.95±0.22[a]	4.27	0.29	4	—	Southern Balearics	Polunin et al. 2001	1
Conger conger (littoral)	33	9.49±0.19	3.78	0.31	2	83.3±1.20	Bay of Calvi	Pinnegar and Polunin 2000	
Muraena helena	33	9.48±0.34	3.78	0.33	3	61.6±6.72	Bay of Calvi	Pinnegar and Polunin 2000	
Nettastoma melanurum	33	12.35	4.00	—	1	—	Southern Balearics	Polunin et al. 2001	
Atheriniformes									
Atherina presbyter	34	7.66±0.12	3.24	0.34	3	5.6±0.32	Bay of Calvi	Pinnegar and Polunin 2000	2
Aulopiformes									
Bathypterois mediterraneus	34	13.09±0.10	3.92	0.30	7	9.5±0.67	Southern Balearics	Polunin et al. 2001	3
Carcharhiniformes									
Galeus melastomus	38	11.21±0.27[a]	3.75	0.33	10	40.4±5.53	Southern Balearics	Polunin et al. 2001	4
Scyliorhinus canicula	38	11.94±0.26[a]	3.97	0.30	5	43.5±1.58	Southern Balearics	Polunin et al. 2001	5
Clupeiformes									
Sardina pilchardis	35	7.86±0.05	3.32	0.33	3	15.8±0.33	Castellammare	This paper	6
Sardinella aurita	35	7.69±0.06	3.18	0.34	3	29.0±1.04	Castellammare	This paper	
Engraulis encrasicholus	35	7.87±0.29	3.16	0.33	5	7.8±0.13	Western Mallorca	This paper	7
Gadiformes									
Gadiculus argenteus	32	9.91±0.26	3.37	0.32	5	9.0±0.38	Southern Balearics	Polunin et al. 2001	8
Micromesistius poutassou	32	10.83±0.10	3.64	0.30	5	—	Southern Balearics	Polunin et al. 2001	9
Phycis blennoides	32	12.52±0.10	4.14	0.29	10	25.1±2.85	Southern Balearics	Polunin et al. 2001	10
Coryphaenoides mediterraneus	32	9.51±0.14[a]	3.25	0.30	2	3.2±0.75[b]	Southern Balearics	Polunin et al. 2001	
Coelorhynchus coelorhynchus	32	11.74±0.14[a]	3.91	0.30	8	6.0±0.00[b]	Southern Balearics	Polunin et al. 2001	11
Coelorhynchus labiatus	32	12.40±0.18	3.71	0.30	4	5.3±0.53[b]	Southern Balearics	Polunin et al. 2001	
Hymenocephalus italicus	32	10.92±0.06[a]	3.67	0.29	6	—	Southern Balearics	Polunin et al. 2001	12
Nezumia aequalis	32	13.84±0.03[a]	4.53	0.29	7	—	Southern Balearics	Polunin et al. 2001	13
Trachyrhinchus trachyrhinchus	32	12.87±0.16	4.16	0.29	3	18.3±0.61	Southern Balearics	Polunin et al. 2001	
Merluccius merluccius	32	9.71±0.04	3.77	0.31	54	19.4±0.21	Castellammare	Badalamenti et al. 2002	14
Lepidion lepidion	32	11.65±0.21[a]	3.88	0.31	8	19.0±3.00	Southern Balearics	Polunin et al. 2001	15
Mora moro	32	12.62±0.05[a]	4.17	0.29	5	42.6±1.30	Southern Balearics	Polunin et al. 2001	
Lophiiformes									
Lophius budegassa	33	11.02±0.16	4.16	0.31	6	23.2±0.82	Castellammare	Badalamenti et al. 2002	16
Myctophiformes									
Lampanictus crocodilus	34	10.05±0.15[a]	3.41	0.31	8	15.5±0.25	Southern Balearics	Polunin et al. 2001	
Notacanthiformes									
Notacanthus bonapartei	33	12.25±0.19[a]	4.06	0.30	9	—	Southern Balearics	Polunin et al. 2001	17
Osmeriformes									
Argentina sphyraena	33	9.69	3.31	—	1	—	Southern Balearics	Polunin et al. 2001	
Alepocephalus rostratus	35	11.42±0.12[a]	3.81	0.30	8	33.8±3.87	Southern Balearics	Polunin et al. 2001	18
Perciformes									
Apogon imberbis	33	9.77±0.17	3.86	0.31	3	11.1±0.40	Bay of Calvi	Pinnegar and Polunin 2000	19

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Seriola dumerili[c]	34	11.51±0.10	4.23	0.29	3	49.3±0.79	Western Mallorca	This paper	20
Trachurus mediterraneaus	34	9.22±0.09	3.63	0.32	3	22.2±1.92	Castellammare	This paper	21
Trachurus trachurus	34	9.45±0.09	3.69	0.31	3	19.7±0.17	Castellammare	This paper	22
Spicara maena	33	7.02±0.32	3.06	0.38	3	17.37±1.32	Bay of Calvi	Pinnegar and Polunin 2000	23
Coryphaena hippurus[c]	34	10.71±0.40	3.99	0.32	5	92.8±3.95	Western Mallorca	This paper	
Epigonus denticulatus	33	10.33	3.49	—	1	—	Southern Balearics	Polunin et al. 2001	24
Pomatoschistus marmoratus	33	11.90±0.10	3.03	0.30	4	10.0±1.50	Upper Adriatic Sea	Camusso et al. 1999	
Coris julis	33	8.60±0.35	3.52	0.34	3	14.1±1.41	Bay of Calvi	Pinnegar and Polunin 2000	25
Symphodus ocellatus	33	8.92±0.23	3.61	0.32	3	8.58±0.14	Bay of Calvi	Pinnegar and Polunin 2000	26
Symphodus roissali	33	10.39±0.21	4.05	0.31	3	10.2±0.81	Bay of Calvi	This paper	
Symphodus tinca	33	8.40±0.40	3.46	0.35	3	19.45±0.20	Bay of Calvi	Pinnegar and Polunin 2000	27
Thalassoma pavo	33	10.31±0.15	3.87	0.31	19	11.13±0.42	Western Mallorca	Jennings et al. 1997	
Liza aurata	34	11.10±0.23	4.18	0.31	2	33.0±0.50	Castellammare	This paper	
Liza ramada	34	7.90±1.33	3.24	0.64	3	34.0±0.29	Castellammare	This paper	
Mullus barbatus	33	10.34±0.15	3.96	0.33	36	14.5±0.18	Castellammare	Badalamenti et al. 2002	28
Mullus surmuletus	33	7.02±17	3.06	0.36	3	17.0±0.22	Bay of Calvi	Pinnegar and Polunin 2000	29
Dicentrarchus labrax (wild)[c]	33	10.33	3.95	—	1	30.0	Capo D'Orlando	This paper	
Dicentrarchus labrax (escapee)	33	12.23±0.03	4.51	0.30	3	27.2±1.09	Castellammare	This paper	
Dicentrarchus punctatus	33	10.28	3.94	—	1	33.0	Castellammare	This paper	
Chromis chromis	33	6.90±0.15	3.02	0.36	3	11.2±0.84	Bay of Calvi	Pinnegar and Polunin 2000	30
Sciaena umbra	33	8.38	3.78	—	1	15.5	Castellammare	This paper	31
Scomber japonicus	37	8.21±0.18	3.33	0.33	3	34.5±2.52	Castellammare	This paper	
Epinephelus marginatus[c]	33	11.32	4.17	—	1	28.4	Western Mallorca	This paper	32
Serranus scriba	33	8.99±0.20	3.64	0.34	3	17.9±2.26	Bay of Calvi	Pinnegar and Polunin 2000	33
Boops boops	33	6.68±0.36	2.96	0.41	3	9.1±1.32	Bay of Calvi	Pinnegar and Polunin 2000	34
Dentex dentex[c]	33	11.36±0.17	4.18	0.29	5	44.4±9.04	Western Mallorca	This paper	35
Diplodus annularis	33	8.39±0.27	3.46	0.34	3	12.5±0.94	Bay of Calvi	Pinnegar and Polunin 2000	36
Diplodus sargus	33	9.13±0.23	3.68	0.32	3	18.5±1.84	Bay of Calvi	Pinnegar and Polunin 2000	37
Diplodus vulgaris	33	10.61±0.26	3.96	0.33	18	17.1±1.24	Western Mallorca	Jennings et al. 1997	38
Oblada melanura	33	9.26±0.12	3.71	0.32	3	21.7±0.90	Bay of Calvi	Pinnegar and Polunin 2000	39
Pagellus acarne	33	11.86±0.14	4.40	0.30	3	17.2±0.33	Castellammare	This paper	40
Pagellus erythrinus	33	11.84±0.31	4.40	0.31	3	19.5±0.00	Castellammare	This paper	41
Sarpa salpa	33	6.97±0.15	3.04	0.36	3	15.9±1.78	Bay of Calvi	Pinnegar and Polunin 2000	42
Sparus aurata (escapee)	33	11.58±0.25	4.32	0.30	2	22.5±0.50	Castellammare	This paper	43
Spondyliosoma cantharus	33	8.50	3.47	—	1	—	Bay of Calvi	Lepoint et al. 2000	44
Sphyraena sphyraena[c]	34	11.53±0.46	4.23	0.31	3	64.8±7.10	Western Mallorca	This paper	
Lepidopus caudatus	37	9.74	3.32	—	1	—	Southern Balearics	Polunin et al. 2001	45
Tripterygion spp.	33	8.03±0.27	3.35	0.34	3	5.1±0.08	Bay of Calvi	This paper	46
Pleuronectiformes									
Bothus podas	31	9.84±0.02	3.81	0.31	3	13.67±0.44	Castellammare	This paper	47
Syphurus ligulatus	31	12.16±0.07	4.03	0.29	6	—	Southern Balearics	Polunin et al. 2001	
Lepidorhombus boscii	31	10.19±0.56	3.45	0.39	5	—	Southern Balearics	Polunin et al. 2001	48
Solea impar	31	10.65±0.09	4.05	0.31	2	18.0±2.40	Castellammare	This paper	
Solea solea	31	12.15±0.03	4.49	0.30	2	34.0±1.50	Castellammare	This paper	49
Scorpaeniformes									
Peristedion cataphractum	33	11.34±0.88	3.79	0.37	2	—	Southern Balearics	Polunin et al. 2001	

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Table A1 (*concluded*).

Order and species	ISSCAAP code	δ^{15}N (±SE)	Trophic level	CV	*n*	Mean size (cm ± SE)	Location	Reference	Figure 2 ID
Scorpaena porcus	33	7.93±0.44	3.32	0.37	3	20.7±2.44	Bay of Calvi	Pinnegar and Polunin 2000	50
Helicolenus dactylopterus	33	11.38±0.22	3.80	0.31	6	—	Southern Balearics	Polunin et al. 2001	51
Chelidonichthys lucerna	33	10.73±0.29	4.07	0.31	3	31.5±0.50	Castellammare	This paper	52
Chelidonichthys obscurus	33	9.07±0.18	3.58	0.32	3	17.8±0.44	Castellammare	This paper	53
Lepidotrigla cavillone	33	9.84±0.07	3.81	0.31	3	11.2±0.17	Castellammare	This paper	54
Squaliformes									
Centrocimnus coelolepsis	38	13.78±0.28	4.12	0.30	3	61.8±2.25	Southern Balearics	Polunin et al. 2001	55
Dalatias licha	38	13.08	4.22	—	1	—	Southern Balearics	Polunin et al. 2001	56
Etmopterus spinax	38	12.77±0.21	4.13	0.29	2	30.0±7.00	Southern Balearics	Polunin et al. 2001	57
Stomiiformes									
Chauliodus sloani	35	9.51±0.14[a]	3.25	0.30	2	26.0±2.50	Southern Balearics	Polunin et al. 2001	
Cyclothone braueri	35	7.63	2.31	—	1	—	Southern Balearics	Polunin et al. 2001	
Stomias boa	35	10.17±0.20[a]	3.45	0.30	2	—	Southern Balearics	Polunin et al. 2001	
Syngnathiformes									
Macroramphosus scolopax	33	12.64±0.25	4.17	0.30	2	—	Southern Balearics	Polunin et al. 2001	
Tetrodontiformes									
Balistes carolinensis	33	7.76±0.13	3.20	0.34	3	16.9±0.60	Castellammare	This paper	
Torpediniformes									
Torpedo torpedo	38	12.49±0.05	4.58	0.30	2	31.5±0.00	Castellammare	This paper	58
Zeiformes									
Zeus faber[c]	33	11.54	4.23	—	1	33.0	Western Mallorca	This paper	59

Note: CV, coefficient of variation; *n*, number of samples; SE, standard error; —, a lack of data. Figure 2 ID provides identifying numbers for data points in Fig. 2.

[a]Situations where deep-sea fish were collected from different depth zones and where δ^{15}N was corrected to "upper slope".

[b]Preanal length measurements (macrourids).

[c]Species collected from local markets.

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Appendix B

Table B1. Database of $\delta^{15}N$ data and trophic level for commercially important invertebrate species.

Species	ISSCAAP code	$\delta^{15}N$ (±SE)	Trophic level	CV	*n*	Location	Reference
Macropipus spp.	42	10.97±0.28	3.68	0.31	3	Southern Balearics	Polunin et al. 2001
Maiidae	42	3.50±0.58	2.00	—	3	Bay of Calvi	Lepoint et al. 2000
Bachyuran crabs (mixed)	42	—	2.99	0.42	5 spp.	Bay of Calvi, Southern Balearics	Lepoint et al. 2000; Pinnegar and Polunin 2000; Polunin et al. 2001
Nephrops norvegicus	43	9.25±0.76	3.18	0.44	3	Southern Balearics	Polunin et al. 2001
Homarus gammarus	43	10.34±0.95	3.96	0.37	2	Castellammare	This study
Palinurid decapods (mixed)	43	—	3.59	0.30	6 spp.	Southern Balearics; Castellammare	Polunin et al. 2001; this study
Palaemon serratus	45	7.80±0.69	3.26	0.42	3	Bay of Calvi	Lepoint et al. 2000
Aristeus antennatus	45	10.39±0.12[b]	3.51	0.32	32	Southern Balearics	Polunin et al. 2001
Parapenaeus longirostris	45	9.97±0.04	3.39	0.30	9	Southern Balearics	Polunin et al. 2001
Nantantian decapods (mixed)	45	—	3.17	0.31	45 spp.	Bay of Calvi, Southern Balearics	Lepoint et al. 2000; Pinnegar and Polunin 2000; Polunin et al. 2001
Anomurid decapods (mixed)	45	—	2.77	0.33	8 spp.	Bay of Calvi, Southern Balearics	Lepoint et al. 2000; Pinnegar and Polunin 2000; Polunin et al. 2001
Bolinus brandaris[a]	52	11.14±0.427	2.81	0.34	3	Upper Adriatic Sea	This study
Haliotis lamellosa	52	2.60±0.857	1.74	1.09	2	Bay of Calvi	Lepoint et al. 2000
Gastropod molluscs (mixed)	52	—	2.06	0.32	17 spp.	Bay of Calvi, Castellammare	Lepoint et al. 2000; Pinnegar and Polunin 2000
Ostrea edulis	53	4.98±0.17	2.38	0.67	5	Castellammare	This study
Crassostrea gigas[a]	53	9.61±0.36	2.36	0.59	3	Upper Adriatic Sea	This study
Mytilus galloprovincialis[a]	54	4.51±0.05	2.24	0.41	3	Lower Adriatic Sea	This study
Ruditapes philippinarum[a]	56	7.33±0.21	1.70	0.46	3	Upper Adriatic Sea	This study
Pecten spp.	55	5.30±0.21	2.53	0.43	2	Bay of Calvi	Lepoint et al. 2000
Cerastoderma edule	56	5.37±0.77	2.49	0.82	2	Castellammare	This study
Acanthocardia aculeata	56	4.49	2.23	—	1	Castellammare	This study
Chamelea gallina	51	5.80	2.62	—	1	Castellammare	This study
Bivalve molluscs (mixed)	53–56	—	2.25	0.32	10 spp.	Bay of Calvi, Castellammare	Lepoint et al. 2000; this study
Histioteuthis bonnelli	57	11.28	3.77	—	1	Southern Balearics	This study
Todarodes sagittatus	57	10.29	3.48	—	1	Southern Balearics	This study
Loligo vulgaris	57	8.17	2.86	—	1	Southern Balearics	This study
Octopus vulgaris	57	10.5	3.54	—	1	Southern Balearics	This study
Eledone moschata	57	9.41±0.18	3.68	0.32	3	Castellammare	This study
Sepia officinalis	57	9.63±0.20	3.75	0.32	3	Castellammare	This study
Cephalopods (mixed)	57	—	3.55	0.30	6 spp.	Southern Balearics, Castellammare	This study
Halocynthia papillosa	73	5.7±0.50	2.65	0.58	4	Bay of Calvi	Lepoint et al. 2000
Holothuria tubulosa	76	5.5±0.35	2.59	0.63	8	Bay of Calvi	Lepoint et al. 2000
Paracentrotus lividus	76	3.6±0.29	2.03	11.18	12	Bay of Calvi	Lepoint et al. 2000
Echinoderms (mixed)	76	—	2.16	0.36	9 spp.	Bay of Calvi	Lepoint et al. 2000; Pinnegar and Polunin 2000

Note: CV, the coefficient of variation; *n*, number of samples; SE, standard error; —, a lack of data.

[a]Species collected from local markets.

[b]Situations in which deep-sea invertebrates were collected from different depth zones and $\delta^{15}N$ was corrected to "upper slope".

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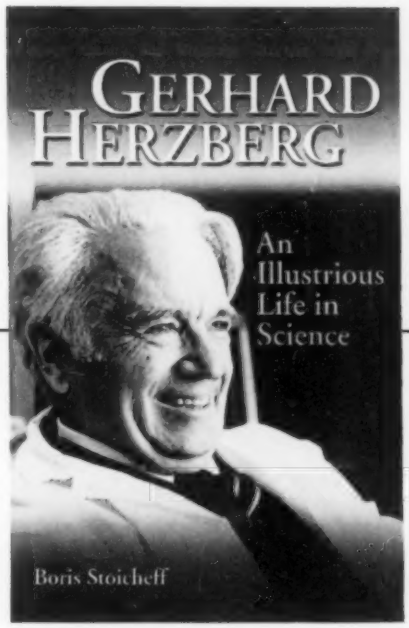

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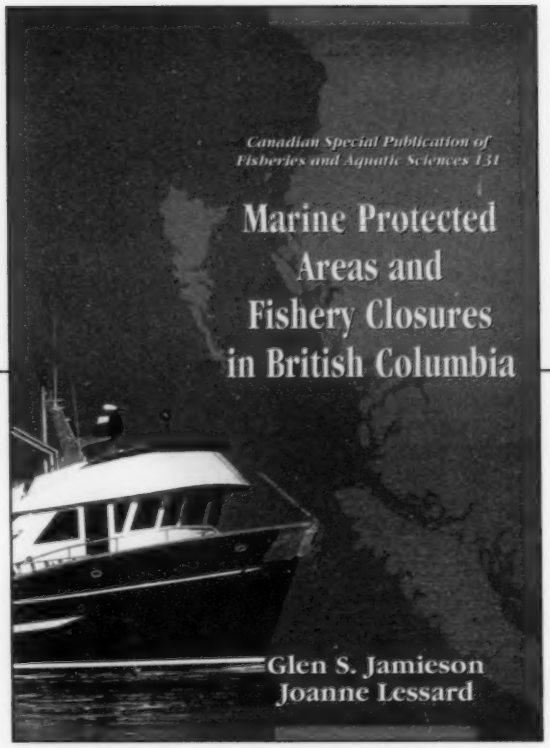
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